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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

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POLYZOA FROM WEST AFRICA

NOTES ON THE GENERA *HIPPOPORINA* NEVIANI, *HIPPOPORELLA* CANU, *CLEIDOCHASMA* HARMER AND *HIPPOPORIDRA* CANU & BASSLER (CHEILOSTOMATA, ASCOPHORA)

By PATRICIA L. COOK

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1. INTRODUCTION

Polyzoa from the north and north-western coasts of Africa and from the neighbouring islands, have been described; but there has been hitherto no systematic collection from the coast of southern Senegal and the Gulf of Guinea. The collections here described consist of the "Calypso" Collection I, from Senegal and the Bay of Biafra, and Collection II, from the Cape Verde Islands; the Marche-Marchad Collections, from Senegal; and the Achimota Collection, from Ghana (see Cook, 1964 : 44).

The holotypes of new species, together with representative specimens of all the material described, are deposited in the British Museum (Natural History).

Material was treated with eau de javelle for examination of calcareous parts, and decalcified and stained to show chitinous parts. The following measurements were made where possible:

Length of zooecium	Lz	Width of operculum	lop
Width of zooecium	lz	Length of avicularium	La
Length of orifice	Lo	Length of mandible	Lm
Width of orifice	lo	Length of ovicell	Lov
Length of operculum	Lop	Width of ovicell	lov

Specimens in the British Museum, Zoology Department, are referred to by their registered numbers, thus: 1911.10.1.1134, and in the Palaeontology Department thus: B 1620.

Species assigned by various authors to *Hippoporina* belong to three distinct genera. These were defined by Harmer (1957 : 977 and 1038), and their synonymies may be summarized as follows:—

1. *Hippoporina* Neviani 1895, type-species *Cellepora pertusa* Esper (= ? *Hippodiplosia* Canu, 1916, type-species *H. verrucosa* Canu, chosen by Hastings, 1930. If *Hippodiplosia verrucosa* is congeneric with *Hippoporina pertusa*, *Hippodiplosia* is a synonym of *Hippoporina*, but this is very doubtful).

2. *Hippoporella* Canu, 1917, type-species *Lepralia hippopus* Smitt (= *Hippoporina*, type-species as used by Canu, 1917, *Lepralia hippopus* Smitt; and *Hippoponella*[1] Canu & Bassler, 1920, type-species *Lepralia hippopus* Smitt).

3. *Cleidochasma* Harmer, 1957, type-species *Gemellipora protrusa* Thornley (= *Hippoporina* Canu & Bassler, 1920, not Neviani, type-species *Lepralia porcellana* Busk).

The genus *Hippoporidra* is similar in character to *Cleidochasma*, but is here confined to species with cortical zooecia and a special type of interzooecial avicularium (see p. 22), which encrust gastropod shells.

2. *HIPPOPORINA* Neviani

Hippoporina Neviani, 1895 : 109. Harmer, 1957 : 977.
Hippodiplosia Canu : Osburn, 1952 : 338.

TYPE SPECIES. *Cellepora pertusa* Esper, 1796 : 149.

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[1] I agree with Hastings (1930 : 724) and Osburn (1952 : 348) in regarding *Hippoponella* as an absolute synonym of *Hippoporella*. The second type-species of *Hippoporella* later chosen by Canu & Bassler (1920 : 377), *Hippoporella perforata*, was not included in the original introduction of the genus by Canu, but is congeneric with *H. hippopus*. Examination of Hincks's figured specimen of *Lepralia hippopus* (1880, pl. 33, figs. 8, 9, 1911.10.1.1134, Northumberland coast, Norman Coll.) which has all the characters of Smitt's description and figures, shows that, contrary to Canu & Bassler's diagnosis of *Hippoponella*, the ovicell is not closed by the operculum.

Diagnosis. Zoarium encrusting. Zooecia with marginal pores and frontal pores, but with the area proximal to the orifice without pores ; lateral and distal septula present. Orifice rounded with a pair of proximal lateral denticles forming a broad sinus, lateral peristome frequently slightly raised. Adventitious avicularia often present. Ovicell hyperstomial, porous, not closed by the operculum.

3. *Hippoporina pertusa* (Esper)

(Text-fig. 1A)

Cellepora pertusa Esper, 1796 : 149, pl. 10, figs. 1, 2, Recent, Mediterranean.

Hippodiplosia pertusa (Esper) Hastings, 1930 : 724, pl. 17, fig. 118, Galapagos, 4–15 fath., Gorgona, Panama. Osburn, 1952 : 340, pl. 40, figs. 5–8, S. California, 17 and 23 fath., Mexico and Galapagos.

Material. *Achimota Coll.* Stn. 47, Dredge haul No. 1, 4.i.51, 44 m., 14V. Stn. 117, Agassiz trawl No. 2, 5.iv.51, 64 m., 32O.

British Museum, Galapagos, 1929.4.26.142, " St. George " Coll. Pt. Vincente, California, 65 ft., 1962.6.16.12, and Gulf of Mexico, 28° 58′ N., 89° 9′ W., 1961.11.2.35, Cheetham Coll., and many other specimens.

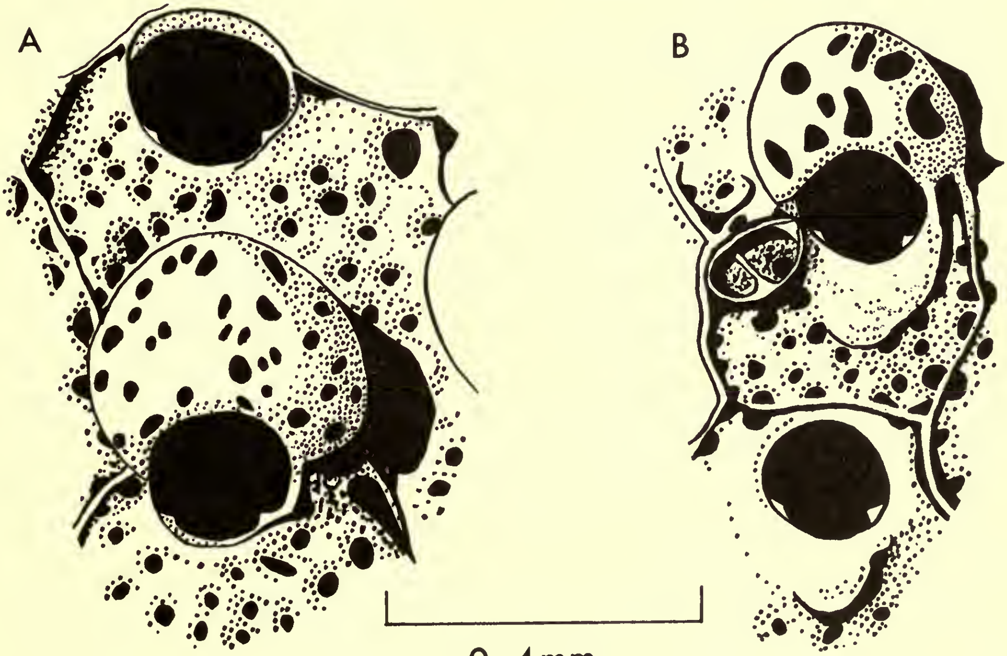

Fig. 1. *Hippoporina*, treated with eau de javelle. A. *H. pertusa*, zooecium and ovicell. Ghana, Achimota Coll. 14V. B. *H. americana*, zooecium and ovicell. Nigeria, 1959.2.20.4.

H. pertusa is not present in the " Calypso " or Marche-Marchad Collections.

Diagnosis. *Hippoporina* with large, wide zooecia. Avicularia usually absent. Ovicells large, wide, pores frequently irregular.

Dimensions. Lz 0·70 mm., lz 0·60 mm., Lo 0·225 mm., lo 0·25 mm., Lov 0·35 mm., lov 0·50 mm.

No avicularia have been seen in any of the material examined. There are 3–4 lateral and 4–5 distal septula, the latter either scattered or in a row near the base of the distal wall.

H. pertusa has a wide geographical distribution extending from the Arctic to California, Florida and Suez (see Hastings, 1930, and Osburn, 1952). The west African specimens show little variation and are very similar to material from Galapagos and the Gulf of Mexico.

4. ***Hippoporina americana*** (Verrill)

(Text-fig. 1B)

Lepralia americana Verrill, 1875a : 415, pl. 7, fig. 4, Long Island Sound to Beverley, Mass., low-water to 30 fath. (not pl. 7, fig. 5 = *Cryptosula pallasiana* (Moll.), see Osburn, 1912 : 241).

Hippodiplosia americana (Verrill) Hastings, 1930 : 725, pl. 11, fig. 61, Balboa, Panama. Marcus 1937 : 101, pl. 20, figs. 54A, B, Brazil, Bahia de Santos, 10–20 m. Osburn, 1952 : 339, pl. 40, fig. 4, Mount Desert, Maine to N. Carolina, and Gulf of California to Costa Rica and Galapagos, 10–30 fath.

Material. *British Museum*, Lagos, Nigeria, 1959.2.18.2, Hill Coll. Port Harcourt, Nigeria, 1959.2.20.3, 4, 6 (on wood, gastropod and oyster shells respectively) ; Freetown, Sierra Leone, 1959.2.20.5 (on *Balanus amphitrite amphitrite* Darwin), Stubbings Coll. W. Africa, 1959.2.22.1, Frewen Coll. Balboa 4, Panama, 1929.4.26.147, " St. George " Coll. Santos, Brazil, 1948.2.16.29, Marcus Coll.

H. americana is not present in the " Calypso " Collections, the Marche-Marchad Collections, or the Achimota Collections.

Diagnosis. Zoarium encrusting, sometimes plurilaminar. Peristome raised laterally, a large umbo frequently present proximally to the orifice. Avicularia often absent, when present with acute mandibles, directed centrally and distally, sub-rostral cavity swollen, with a complete bar.

Dimensions. Lz 0·38 mm., lz 0·30 mm., Lo 0·12 mm., lo 0·12 mm., Lm 0·05 mm., Lov 0·20 mm., lov 0·225 mm.

There are 3–4 lateral and 4 distal septula, about one-third of the way up the distal wall. The avicularia appear to arise secondarily, as in several cases the swollen sub-rostral chamber, when developing or broken, shows the frontal pores beneath it (see Text-fig. 1B). The bar supporting the mandible is slender, and is frequently broken even in slightly worn specimens. The ovicell is often very lightly calcified frontally, and the pores may be very large and irregular.

H. americana appears to be tolerant of a wide range of temperature and of slightly lowered salinity, the west African localities listed above being associated with river estuaries and saline lagoons.

5. ***Hippoporina lacrimosa*** sp. n.

(Text-fig. 2A)

HOLOTYPE. B.M. 1963.4.16.4, Achimota Coll., Stn. 47.

MATERIAL. *Marche-Marchad Coll. I*, 39E, Baie de Seminoles, Gorée, 8.xii.53, 38 m., growing over the convex surface of *Cupuladria* sp. 39A. Coll. II, 25F, S.W. du Cap. Manuel, Dakar, 20.ii.56, on *Cellepora* sp. 25D. *Achimota Coll.* Stn. 47, Dredge haul No. 1, 4.i.51, 44 m., 14S, Paratypes, and Stn. 48, as above, No. 2, 44 m., 46J. Stn. 110, Agassiz trawl, No. 1, 4.iv.51, 40 m., 48L. Stn. 111, as above, No. 2, 43 m., 49B. Stn. 112, as above, No. 3, 43 m., 60J. Stn. 132, as above, 2.v.51, 44 m., 40D and 42J.

H. lacrimosa is not present in the " Calypso " Collections.

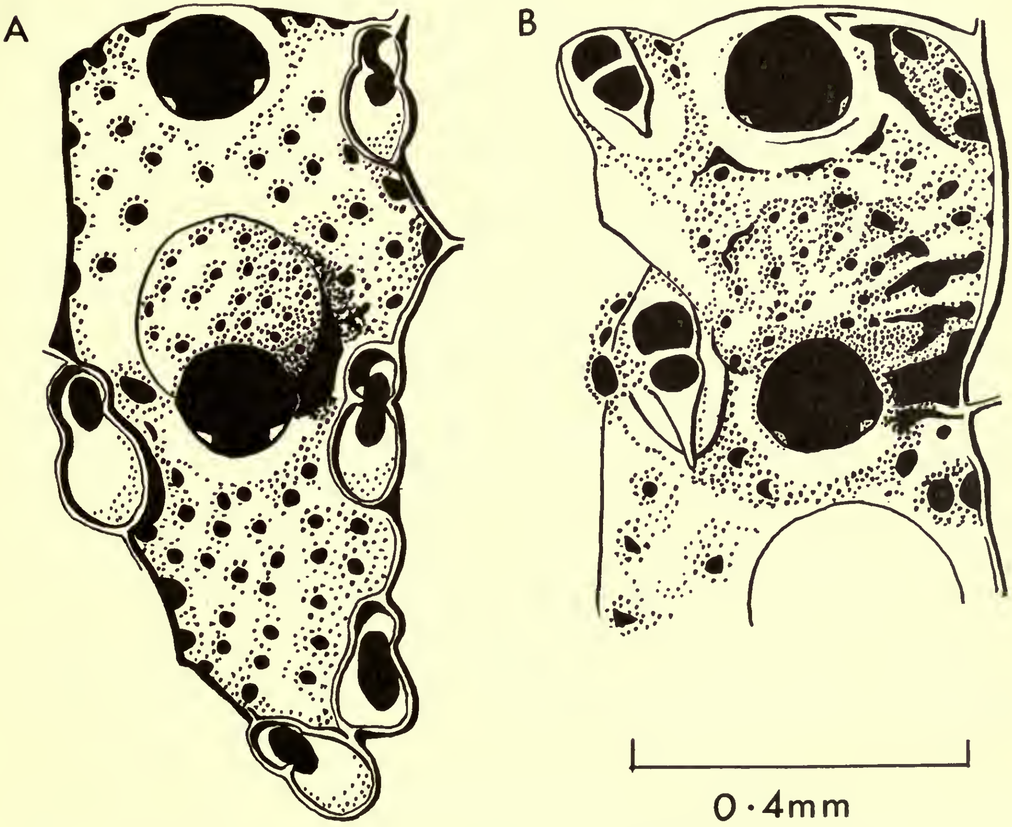

FIG. 2. *Hippoporina*, treated with eau de javelle. A. *H. lacrimosa*, zooecia with avicularia, and ovicell. Ghana, Achimota Coll. 14S. B. *H. acuta*, zooecium with avicularia, and ovicell. Ghana, Achimota Coll. 59D.

DIAGNOSIS. Zoarium encrusting. Small lateral peristomial tubercles and sub-oral umbo frequently present. Avicularia sometimes paired, sub-rostral cavity slightly swollen, with a delicate bar. Rostrum and mandible broadly spathulate, directed proximally. Ovicell porous, prominent, occasionally extending over two distal zooecia.

Dimensions. Lz 0·50 mm., lz 0·35 mm., Lo 0·11 mm., lo 0·125 mm., Lm 0·10 mm., Lov 0·20 mm., lov 0·27 mm.

The distal communication pores of *H. lacrimosa* differ from those of the other species as they are so low on the wall that they may pass through the angle between the distal and basal walls. In these cases, secondary calcification round the pores produces an appearance very similar to that of dietellae.

6. ***Hippoporina acuta*** sp. n.

(Text-fig. 2B)

HOLOTYPE. B.M. 1963.4.16.5, Achimota Coll. Stn. 35.

MATERIAL. *Achimota Coll.* Stn. 35, Dredge No. 1, 21.xii.50, 37 mm., 59D (on *Jullienella foetida*), Paratypes. Stn. X, Axim, Hospital reef, 7.i.51, 68J (with 68E *Hippoporidra littoralis* see p. 28).

" Calypso " Coll. I. Stn. 114, devant baie 8. Antonio, 8.vii.56, 50 m., C 15 O.

H. acuta is not present in the " Calypso " Collection II from the Cape Verde Islands, or in the Marche-Marchad Collections.

DIAGNOSIS. Zoarium encrusting. Zooecia similar to those of *H. lacrimosa.* Avicularia sometimes paired, lateral to the orifice, sub-rostral cavity very swollen ; with a complete bar, directed proximally and centrally. Mandible triangular, acute, curved. Ovicell porous, less prominent than in *H. lacrimosa.*

Dimensions. Lz 0·40 mm., lz 0·30 mm., Lo 0·11 mm., lo 0·12 mm., Lm 0·10 mm., Lov 0·20 mm., lov 0·32 mm.

H. acuta resembles the figure of *Hippothoa reversa* (Verrill 1875b : 41, pl. 3, fig. 1, Gay Head, New England), but differs in the inward orientation of the avicularia. *H. acuta* and *H. lacrimosa* are very similar but no form intermediate to the two very different types of avicularia has been seen. The two species also differ in the position of the distal septula, which in *H. acuta* are like those of *H. americana* ; and in the wider, less prominent ovicells of *H. acuta.* The oral denticles of *H. acuta* are slightly more proximal in position than those of *H. lacrimosa.*

Material of both species in the Achimota Coll. encrusts the Foraminiferan, *Jullienella foetida* Schlumberger, and thus belongs to the silty-sand community of Buchanan (1958) and Bassindale (1961).

7. ***HIPPOPORELLA*** Canu

Hippoporella Canu, 1917 : 36. Osburn, 1952 : 348.
Hippoponella Canu & Bassler, 1920 : 379.

TYPE-SPECIES. *Lepralia hippopus* Smitt, 1868 : 20, 127, pl. 26, figs. 99–105, Spitzbergen and Finmark.

DIAGNOSIS. Zooecia small, frontal pores rare. Orifice with oral spines and a pair of small proximal-lateral denticles, proximal margin slightly curved. Small adventitious avicularia and occasional vicarious avicularia present. Ovicells imperforate, not closed by operculum.

8. ***Hippoporella gorgonensis*** Hastings

(Pl. 1, fig. 1, Text-fig. 3A)

Hippoporella gorgonensis Hastings, 1930 : 723, pl. 12, figs. 62–72, pl. 17, figs. 119, 121, Galapagos Coiba, and Gorgona, shore to 15 fath. Marcus, 1937 : 99, pl. 19, figs. 53A, B, Brazil, Bahia de Santos, 20 m. Soule, 1961 : 20, Gulf of California, 1–17·5 fath.

HOLOTYPE. B.M. 1929.4.26.137, Gorgona.

MATERIAL. *Achimota Coll.* Stn. 35, dredge haul No. 1, 21.xii.50, 37 m., 59O. Stn. 72, as above, No. 3, 24.i.51, 38 m., 61O. Stn. 110, Agassiz trawl No. 1, 4.iv.51, 40 m., 48S. Stn. 133, as above, No. 3, 2.v.51, 51 m., 45U. Stn. K, on trawl debris, 1 mile offshore, 2 miles beyond Densu, 2.iii.49, 36G and 44H.

British Museum, Galapagos, 1929.4.26.130, 131, 134–136, 139, 141. Gorgona, 1929.4.26.132, 133, 137. Coiba, 1929.4.26.161. Taboga, 1929.4.26.138. Jicaron, 1929.4.26.140, " St. George " Coll. Santos Brazil, 1948.2.16.30 and Guariyá, Brazil, 1948.2.16.78, Marcus Coll.

H. gorgonensis is not present in the " Calypso " or the Marche-Marchad Collections.

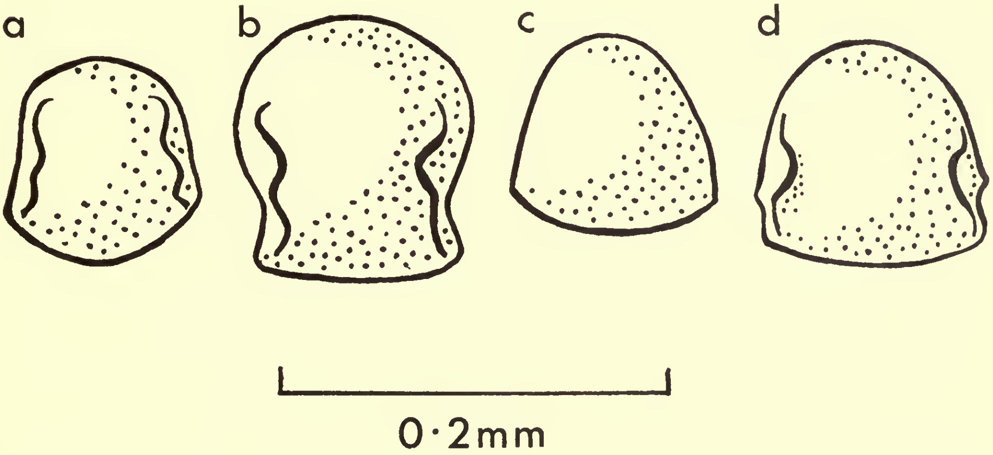

FIG. 3. Opercula in *Hippoporella*. A. *H. gorgonensis*, Ghana, Achimota Coll. 44H. B. *H. hippopus*, Kola peninsula, 1899.7.1.1430. C. *H. multidentata*, Siboga Coll. Sulu archipelago, 62O. D. *H. pusilla*, Cape Verde Islands, 1926.10.1.19.

DIAGNOSIS. Zoarium encrusting, plurilaminar. Zooecia with marginal pores but no frontal pores, and 2–4 lateral and distal septula, the latter low on the distal wall. Orifice with 4 oral spines and a pair of minute proximal-lateral denticles, proximal border nearly straight ; surrounded by lateral and proximal umbos. Avicularia adventitious, frequent, variable, usually paired, one each side of the orifice, occasionally larger, variously orientated. Ovicell hyperstomial, not porous, frequently with a spiked umbo on the front.

Dimensions. Lz 0·30 mm., lz 0·25 mm., Lo 0·08 mm., lo 0·08 mm., Lm 0·04 mm., Lov 0·12 mm., lov 0·20 mm.

The young zooecia at the growing edge may be without avicularia or umbos surrounding the orifice, they consequently have a very different appearance to those in older parts of the colony (see Hastings, 1930 : 723). The opercula of the west African specimens appear to be of the type with curved lateral sclerites figured by Hastings (1930, pl. 12, fig. 72) ; they are very similar to those of *H. hippopus* (Kola Peninsula, 1899.7.1.1430, Busk. Coll.). *H. gorgonensis* is very similar to specimens of *H. multidentata* (see Harmer, 1957 : 1090, pl. 73, figs. 9–12), from Ceylon (1936.12.30.41A) and India (1936.12.30.117), but opercula of *H. multidentata* from the Sulu Archipelago (Siboga Coll. 620), do not have any lateral sclerites (see Text-fig. 3C). *H. gorgonensis* has 4 oral spines and *H. multidentata* has 6. When an ovicell is present the number of spines is reduced to 2 in *H. gorgonensis* and 4 in *H. multidentata.* Avicularia are present on the ovicelled zooecia of *H. gorgonensis*, but absent in *H. multidentata.* Harmer noted that the ovicells of *H. gorgonensis* had a " more complete frontal wall " than those of *H. multidentata.*

H. gorgonensis has not been previously reported from the eastern Atlantic.

9. ***Hippoporella pusilla*** (Smitt)

(Text-fig. 3D)

Discopora albirostris forma *pusilla* Smitt, 1873 : 70, pl. 12, fig. 233, Florida, 9–60 fath.
Cellepora sexspinosa Waters, 1899, pl. 3, fig. 12, Madeira (no description). Norman, 1909 : 311.
Lepralia watersi Calvet, 1906b : 216 ; 1907 : 412, pl. 27, fig. 11, Cape Verde Islands, 20–25 m.
Holoporella pusilla (Smitt) Waters, 1918a : 22, pl. 2, figs. 7–9, Cape Verde Islands, 10 fath.

MATERIAL. " *Calypso* " *Coll. II.* Stn. 26, 15° 16′ 30″ N., 23° 47′ 31″ W., 18.xi.59, 50–65 m., île Sao Tiago, C65I. Stn. 42, Punto do Anciao, 20.xi.59, 15–30 and 60 m., C104E. Stn. 75, 16° 04′ 20″ N., 22° 58′ 10″ W., 25.xi.59, 45 m., C106F. Stn. 86, 16° 36′ 20″ N., 22° 52′ 05″ W., 26.xi.59, 25 m., C71E.

British Museum, Cape Verde Islands, 1926.10.1.19, Waters Coll.

Museo do Seminario, Funchal. 1 slide, Type of *C. sexspinosa* Waters.

Hippoporella pusilla is not represented in the Marche-Marchad or Achimota Collections.

DIAGNOSIS. Zoarium encrusting, plurilaminar. Zooecia larger than those of *H. gorgonensis* or *H. multidentata.* Orifice lepralioid with a large sub-oral umbo, a pair of distinct oral denticles and 6 long oral spines. One or two small avicularia near the orifice, with pointed mandibles, directed distally. Occasionally other adventitious avicularia present. Ovicell small, finely tuberculate, raised above the orifice and wide open frontally.

Dimensions. Lz 0·45 mm., lz 0·30 mm., Lo 0·10 mm., lo 0·10 mm., Lm 0·06 mm., Lov 0·10 mm., lov 0·15 mm.

Calvet tentatively suggested that his *L. watersi* was synonymous with *C. sexspinosa*, and Waters, in describing material from the Cape Verde Islands stated that *L. watersi* was identical with both *C. sexspinosa* and *H. pusilla.* The type of *C. sexspinosa* is a very young colony without ovicells, but shows the long oral spines. Harmer

(1957 : 1097) considered that the ovicells of *H. pusilla* were unlike those normally found in *Hippoporella*, but the ovicells of Waters's Cape Verde Islands specimens (1926.10.1.19) are similar to those of *H. multidentata*. They are small and very open frontally, and significantly narrower than those of *H. gorgonensis*. In ovicelled zooecia, only one pair of spines is present, thus differing from *H. multidentata*. The large umbo below the orifice is not accompanied by lateral processes, as in *H. gorgonensis*. *H. pusilla* differs from both *H. gorgonensis* and *H. multidentata* in the form of the operculum and Hastings (1930 : 724) remarked on the differences between the opercula of these two species. Those of *H. pusilla* are the larger, with a nearly straight proximal edge, and with a pair of very short lateral sclerites, ending distally in strong protuberances which articulate with the oral denticles. These protuberances give the operculum the characteristic notched appearance figured by Waters (1918a, pl. 2, fig. 8), and see Text-fig. 3D.

10. ***CLEIDOCHASMA*** Harmer

Cleidochasma Harmer, 1957 : 1038. Soule, 1961 : 18.

Type species. *Gemellipora protrusa* Thornley, 1905 : 119, pl. 7, Ceylon.

Diagnosis. Zoarium plurilaminar, encrusting or erect. Orifice cleithridiate, with a pair of well-developed condyles. Oral spines frequently present.[1] Marginal and a few frontal pores present, lateral and distal uniporous septula, or multiporous rosette plates or dietellae present. Interzooecial and adventitious avicularia present. Ovicell hyperstomial, with a frontal area, not closed by the operculum.

11. ***Cleidochasma porcellanum*** (Busk)

(Pl. 1, fig. 4, Pl. 2, figs. 1, 2, Text-figs. 4A–E)

Lepralia porcellana Busk, 1860 : 283, pl. 31, fig. 3, Madeira.
Lepralia cleidostoma Smitt, 1873 : 62, pl. 11, figs. 217–219, Florida, 30–120 fath.
Hippoporina porcellana (Busk) Hastings, 1930 : 722, Taboga, Gorgona, Galapagos, 1–30 fath., synonymy. Sakakura, 1935 : 23, pl. 4, fig. 6, Pleistocene, Japan. Marcus, 1937 : 96, pl. 19, fig 51, Brazil, Santos, 20 m.; 1938 : 217, text-fig. 17, St. Helena, 27–55 m., synonymy and distribution. Osburn, 1952 : 344, pl. 41, figs. 1–3, southern California to Callao, Peru.
Hippoporina simplex Canu & Bassler, 1930 b: 49, pl. 6, figs. 3, 6, Tunisia.
Hippoporina bassleri Calvet, 1931 : 84, pl. 2, figs. 33A–C, Cape Verde Islands.
Cleidochasma bassleri (Calvet) Harmer, 1957 : 1042, pl. 71, figs. 5, 16, East Indies, synonymy and distribution.
Cleidochasma porcellana [sic] (Busk) Soule, 1961 : 18, Gulf of California, 1–45 fath.

Lectotype. Chosen here, B.M. 1899.7.1.1726, Madeira, Busk. Coll.

Lectoparatypes. 1899.7.1.1727, 1728.

Material. "*Calypso*" *Coll. I.* Stn. 3, 13° 1′ N., 17° 24′ W., 15.v.56, 51–55 m., C54F. Stn. 25, 4° 36′ 5″ N., 1° 31′ W., 24.v.56, 50 m., C10H. Stn. 26, 4° 37′ N., 0° 50′ W., 24.v.56, 100–90 m ., C17B (on shell). Stn. 45, 0° 25′ N., 9° 0′ E., 8.vi.56, 73 m., C48E on 48A and D, *Discoporella* spp., and C55C on 55F, *C. brancoense*, and 55E, *Hippoporidra senegambiensis*. Stn. 110, off Principe, 7.vii.56, C9L (on shell).

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[1] Oral spines are apparently absent in *C. protrusum* and *C. rotundorum*, but are present in the other species described here.

Stn. 114, devant B. de Sao Antonio, 8.vii.56, 50 m., C15B. Stn. P2, entre Pte. da Mina et I. S. Ana, 4.v.56, 8–10 m., C8H (on shell). Stn. P3, devant Cais de S. Ana, 26.vi.56, 11 m., C19A (on shell). *Coll. II.* Stn. 24, 15° 16′ 34″ N., 23° 47′ 44″ W., 55–60 m., 95E, 100E. Stn. 26, 15° 16′ 30″ N., 23° 47′ 31″ W., 50–65 m., 121N, 125N. Stn. 65, 15° 37′ N., 25° 69′ W., 150–120 m., 67D.

Marche-Marchad Coll. I. Cap Matakong, Guinée Ise., 4 I, on shell with *C. oranense* and other species.

Achimota Coll. I. Stn. 126, Agassiz trawl No. 3, 12.iv.51, 16 m., 37G (on shell). Stn. K, on trawl debris, 1 mile offshore, 2 miles W. of Densu R., 2.iii.49, 4 fath., 36I and 44E (on shell).

Coll. II. Chorkor, seine net, 1.ii.50, 22N (on worm tubes and shell).

British Museum, Madeira, 1899.7.1.1726, 1727, 1728, 2352, 2353, Busk. Coll. Madeira, 1910.11.1.1112A & C (with *C. contractum*), 1115 ; Santa Cruz, 115 fath., 1910.11.1.1116 ; Grenada, 170 fath., 1910.11.1.1113 ; Havana, 1910.11.1.1114A, Norman Coll. John Adams Bank, off Brazil, 1899.7.1.3347, Busk. Coll. Bahia, 1899.5.1.800, Hincks Coll. Gulf of Mexico, 1932.3.7.87, Canu & Bassler Coll. Gulf of Mexico, 1959.8.20.9, Lagaaij Coll. South pass of Mississippi R., 28° 58′ N., 89° 8′ W., 1961.11.2.25, and Campeche Bank, 1961.11.2.22, 23, 24, Cheetham Coll. Gorgona, 1929.4.26.126, "St. George" Coll. Galapagos, 1933.12.10.26, Canu & Bassler Coll. Tizard reef, China Sea, 1889.8.21.65. Alexandria, 1963.8.2.37, O'Donoghue Coll. Ceylon, 1936.12.30.34A, Thornely Coll. Philippines, 1931.12.30.114, 115, Canu & Bassler Coll. Siboga Coll., all specimens listed by Harmer (1957 : 1042).

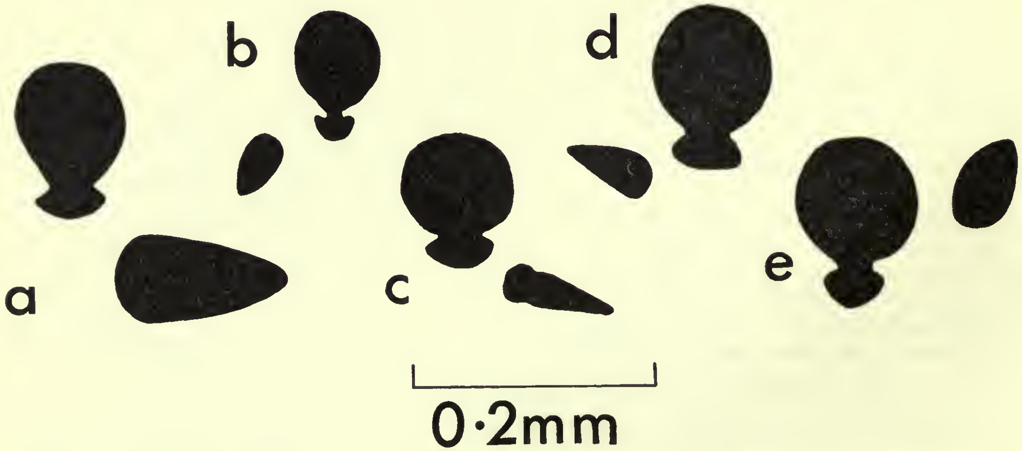

FIG. 4. Variation in shape of orifice and position of avicularia in *Cleidochasma porcellanum*. A. Campeche Bank, Gulf of Mexico, 1962.11.2.22. B. Ceylon, 1936.12.30.34A. C. Bay of Biafra, "Calypso" Coll. C55C. D. Madeira, 1899.7.1.1726. E. Tizard Reef, 1889.8.21.65.

Museu do Seminario, Funchal, 1 slide in Waters Collection.

Naturhistoriska Riksmuseet, Stockholm. No. 284, W. of Tortugas, 16.i.1869, 42 fath. ? Type of *Lepralia cleidostoma*.

DIAGNOSIS. Zoarium encrusting, plurilaminar. Zooecia with marginal pores and porcellanous, smooth or mammillate frontal, 3–4 lateral and distal septula. Orifice with 3 oral spines, cleithridiate, very variable in shape. Operculum with 2 lateral sclerites. Avicularia frequently paired, with a complete bar, situated at or below the level of the sinus, directed outwards and upwards, mandible acute. Ovicell with a small area on the proximal border.

Dimensions. Lz 0·45 mm., lz 0·30 mm., Lo 0·14 mm., lo 0·11 mm., Lop 0·14 mm., lop 0·10 mm., Lav. 0·09 mm., Lm 0·05 mm., Lov 0·15 mm., lov 0·19 mm.

The appearance of *C. porcellanum* varies considerably with the nature of the frontal wall, the position, dimensions and proportions of the orifice, the size and position of the avicularia, and the age and degree of calcification of the ovicells.

The frontal wall was described by Busk as " uneven, bossed, granular, polished, porcellanous ". Busk's colonies show two types of frontal, although the other zooecial characters are the same. In 1899.7.1.1726 the frontal is hyaline and smooth, in 1899.7.1.1727 and 1728 it is mammillated, and greatly resembles the figure of *H. bassleri* given by Calvet. Mammillate frontals are also present in 1961.11.2.25, Gulf of Mexico, 1899.7.1.2352 and 2353, Madeira, and 1889.8.21.65, Tizard Reef, but in the majority of specimens the zooecia are smooth.

The variation in the shape of the orifice is very great, and several forms have been recognized. Some orifices are elongated, with a small triangular sinus, others are rounded with a wide, shallow sinus (see Text-figs. 4A–E). However, these extremes may occur within one zoarium (e.g. 1936.12.30.34A), and intermediate forms exist throughout the material. Furthermore, there appears to be no positive correlation of orifice type with locality or depth. *C. porcellanum* thus differs from the 3 species of *Hippoporidra* described below (pp. 28–32), where the different forms of the orifice are exclusive and are correlated with other distinguishing characters.

The orifice may be surrounded by one proximal and a pair of lateral raised umbos (1899.7.1.1728 and Achimota Coll. 22N). Hastings (1930 : 722) expressed doubt as to the validity of the position of the orifice with relation to the distal wall as a specific character. The orifice is near the distal edge of the zooecium in Siboga Coll., Japan, 53 fath., Owston Coll. 2X ; 1911.10.1.1112, Madeira ; 1899.5.1.800, Bahia ; and 1931.12.30.114, Philippines. It is appreciably removed from the distal edge in Siboga Coll., Torres Straits, Haddon Coll. 173 ; Achimota Coll. 44E ; 1936.12.30.34, Ceylon and 1933.12.10.26, Galapagos. Waters (1899 : 10, pl. 3, figs. 16, 17) mentioned the large variation in the opercula, which may also be seen in the figures of Smitt (1873, pl. 11, figs. 217, 218, 219) and Canu & Bassler (1920, text-fig. 114B–E ; 1929, text-fig. 132B–H).

The size and position of the avicularia varies considerably (see Text-fig. 4A–E). In many specimens (or even parts of one colony) they are minute or absent, in others they are larger, with elongated triangular mandibles, which may be curved or flat. Their position varies, from one close to the orifice to one near the borders of the zooecium, and from level with the poster to below the sinus, sometimes within one specimen (e.g. 1936.13.30.34A pt., Ceylon). Occasionally some zooecia have a large avicularium, with a mandible similar to that of *C. laterale* Harmer (1957 : 1044, pl. 71, figs. 9–11), e.g. 1911.10.1.1116 Santa Cruz, and 1961.11.2.22, Campeche Bank.

Near the growing edge the ovicells are conspicuous and hyaline, with a distinct, thinner, frontal area, and frequently with paired channels on the proximal lateral border which may mark the former position of the oral spines. At this stage, the ovicell may be faintly striated, with lines of slightly thicker calcification below the surface which reflect light differentially. Later the surface becomes finely tuberculate and finally the ovicell is progressively immersed by heavy secondary calcification. Striated ovicells were figured by Smitt (1873, pl. 11, fig. 217) who, however, also showed an older, immersed ovicell (fig. 218). Smitt's specimen has been re-examined and a photograph of one of the young striated ovicells is given on pl. 2, fig. 1 for comparison with fig. 2. Striated ovicells are present in the following specimens :—Achimota Coll. 44E ; " Calypso " Coll. II C125N ; 1911.10.1.1112, Madeira ; 1899.9.7.1.3347, John Adams Bank ; and Siboga Coll., Ceylon, Thornely Coll. 55.

Norman (1909 : 305) first equated *L. cleidostoma* Smitt with *L. porcellana* Busk, and Calvet (1931 : 84) stated that the avicularia of *H. bassleri* were similar to those of the other two species and remarked " Ce sont des formes voisines ". Harmer (1957 : 1042) established a very wide range of variation for *C. bassleri*, but all the Pacific and Indian Ocean records he included had been placed in *H. porcellana* by Marcus (1938 : 217) who distinguished *H. bassleri* by its more constricted operculum and regularly mammillate frontal. Neither of these distinctions appears now to be specific. *C. bassleri* was originally described from the Cape Verde Islands and *C. porcellanum* from Madeira, and thus both species also have similar eastern-Atlantic type-localities. The conclusion is inevitable that *C. porcellanum* (Busk) varies in a similar degree to, and indeed includes, *C. bassleri* (Calvet).

The distal septula in *C. porcellanum* are small and slit-like, close to the base of the wall. The basal lamina of the growing edge is frequently ridged vertically on either side of each pore, forming a chamber. This development may be seen particularly well in " Calypso " Coll. C95E. Thus the distal " chambered pore " of *C. porcellanum* resembles both the sunken rosette plates of *C. protrusum* and the true dietellae of *C. contractum*. A similar variation in position and relationships of the distal pores is found in *Hippoporina* (see p. 8).

12. ***Cleidochasma contractum*** (Waters)

(Text-fig. 5A)

Lepralia contracta Waters, 1899 : 11, pl. 3, figs. 4–6, Madeira. Norman, 1909 : 306, pl. 41, figs. 5, 6, Madeira.

Perigastrella contracta (Waters): Hastings, 1930 : 722, pl. 11, fig. 60, Galapagos, 10–30 fath., Gorgona. Marcus, 1937 : 98, pl. 20, figs. 52A, B, Brazil, Santos, 20 m., synonymy and discussion.

Hippoporina contracta (Waters) : Osburn, 1940 : 428 ; 1952 : 346, pl. 41, figs. 4–5, Ecuador to Gulf of California. Marcus, 1955 : 298, Espirito Santo, 35 m.

Cleidochasma contracta [sic] (Waters) Soule, 1961 : 19, Gulf of California, 1–40 fath.

The type-material of *C. contractum* is preserved in the Museo do Seminario, Funchal, Madeira (see Norman, 1909 : 306).

MATERIAL. "*Calypso*" *Coll. I.* Stn. 4, 12° 55′ N., 17° 33′ W., 16.v.56, 65–75 m., C3C (on sandy worm-tubes with *Rhynchozoon* sp.). Stn. 17, 5° N., 5° 28′ 30″ W., 21.v.56, 27 m., C56E (on *Jullienella foetida*). Stn. 110, 1° 2′ 45″ N., 7° 17′ 34″ E., 7.vii.56, 25–40 m., G. Frère N.E., C32A (on stem of alga). Stn. 114, devant B. de Sao Antonio, 8.vii.56, C15C. Stn. T5, à l' E. Ste Diego, 7.v.56, nunes à pied, C26A. *Coll. II.* Stn. 14, 14° 53′ 43″ N., 23° 31′ 24″ W., 17.xi.59, 25–30 m., C68G. Stn. 24, 15° 16′ 34″ N., 23° 47′ 44″ W., 18.xi.59, 55–60 m., C91H, C97D, and C98D. Stn. 25, 15° 16′ 30″ N., 23° 47′ 31″ W., 18.xi.59, 50–65 m., C121D.

Marche-Marchad Coll. II. 3A, no information (on *Murex* shell).

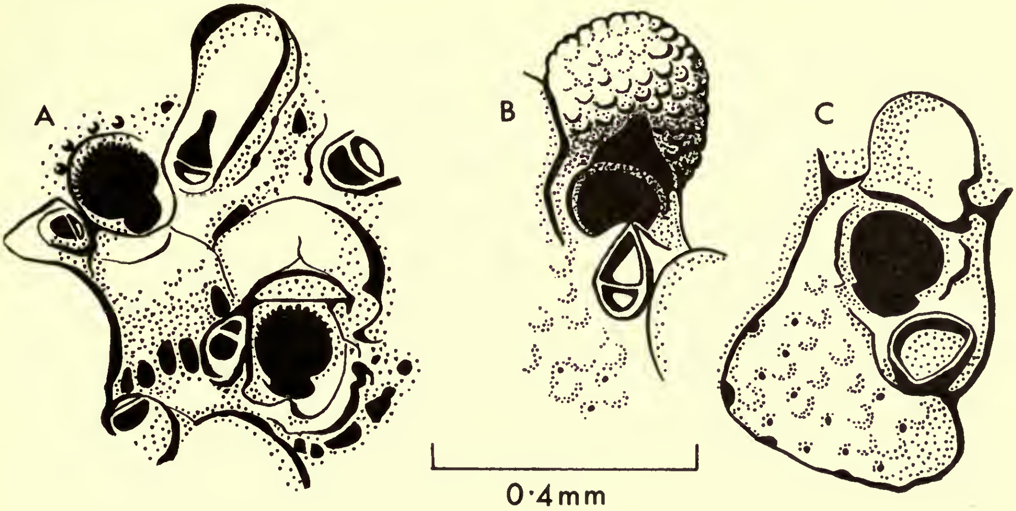

FIG. 5. *Cleidochasma*, treated with eau de javelle. A. *C. contractum*, zooecia, with large spathulate, and small avicularia, and ovicell, Ghana, Achimota Coll., C, F. B, C. *C. rotundorum*, B. Ovicell. C. Zooecium with basal wall of broken ovicell, Madeira, 1911.10.1.1664.

Achimota Coll. I (all specimens on *J. foetida*). Stn. 35, dredge haul No. 1, 21.xii.50, 37 m., 59B. Stn. 45, as above, No. 5, 22.i.51, 22 m., 62K. Stn. 47, as above, No. 1, 4.i.51, 44 m., 14U. Stn. 48, as above, No. 2, 46L. Stn. 72, as above, No. 3, 24.i.51, 38 m., 61I. Stn. 73, as above, No. 4, 41 m., 58G. Stn. 110, Agassiz trawl, No. 1, 4.iv.51, 40 m., 48N. Stn. 111, as above, No. 2, 43 m., 49D. Stn. 112, as above, No. 3, 60L. Stn. 131, as above, No. 1, 2.v.51, 37 m., 41M, 43M. Stn. 132, as above, No. 2, 44 m., 40F and 42L. Stn. 133, as above, No. 3, 51 m., 45N. Specimen C, F, Achimota.

Coll. II. 23Q, Seine net, Chorkor shore, 12.v.50.

British Museum, Madeira, 1911.10.1.1112A (with *C. porcellanum*), 1156 and 1160 (on clinker), and Havana, 80 fath., 1911.10.1.1114, Norman Coll. St. Vincent, Kingstown Harbour, 1931.5.2.5 pt., Totton Coll. Galapagos, 1929.4.26.189, " St. George " Coll. Campeche Bank, 24° 4′ N., 91° 50′ W., 26 fath., 1961.11.2.16, and S. Pass of Mississippi R. 28° 4′ N., 58′ N., 89° 9′ W., 1961.11.2.15, Cheetham Coll. Mauritius, 1934.10.6.24.

Museo do Seminario, Funchal, 1 slide, Type of *L. contracta* Waters.

DIAGNOSIS. Zoarium encrusting, plurilaminar. Zooecia with marginal pores only, dietellae present. Orifice with 4–8 oral spines and a strongly beaded rim, with a pair of strong denticles marking a rounded sinus. Avicularia with a bar, very variable in size and occurrence, occasionally absent from areas of the colony. Usually one or two rounded avicularia, or one large sub-oral or lateral avicularium, with a spathulate mandible. Ovicells hyperstomial with a large semi-circular area on the front.

Dimensions. Lz 0·41 mm., lz 0·33 mm., Lo 0·11 mm., lo 0·10 mm., Lm 0·03–0·23 mm., Lov 0·18 mm., lov 0·20 mm.

The type-species of *Perigastrella* Canu & Bassler (1917 : 68) is " *Lepralia labiata* Boeck, 1861 ". Boeck (1862 : 49–50) did not describe this species, which was introduced by Smitt (1868 : 27, 175). Osburn (1940 : 428) gave reasons for separating *L. contracta* from *Perigastrella*, and placed the species in *Hippoporina* (Canu & Bassler not Neviani, see p. 4). Harmer (1957 : 823 and 1025) emphasized that *L. labiata* and *L. contracta* were not congeneric.

The variability in appearance of *C. contractum* is principally dependent upon the development of the avicularia. At the growing edge of a colony the zooecia frequently have only a small sub-oral umbo, and avicularia are absent, as Waters noted (1899 : 11). The lateral peristome is sometimes slightly raised laterally. Where conditions of growth are crowded, or where the colony is plurilaminar and secondary calcification has taken place, the orifices are immersed and there is a large number of avicularia, some of which may obscure the orifice altogether. The specimens from Havana (1911.10.1.1114) and Mauritius (1934.10.6.24) have a large avicularium directed distally alongside the orifice in the same manner as that of the specimen from Madeira figured by Waters (1899, pl. 3, fig. 4). Examination of the figured slide shows that this type of avicularium is associated only with fertile zooecia. Specimens from the Achimota Coll. have a large avicularium either lying across the proximal edge of the orifice or pointed distal-laterally, whereas many of those from the Cape Verde Islands (" Calypso " Coll. II) have only small rounded avicularia and a sub-oral umbo. However variable the superficial appearance of the colonies, *C. contractum* may always be recognized by the beading round the distal edge of the orifice, and by the large semicircular area on the front of the ovicell.

The occurrence of distinct dietellae in *C. contractum* was noted by Hastings (1930 : 739, expl. of pl. 11, fig. 60). The communications in *Cleidochasma* are very variable ; in *C. protrusum* (Thornely), (Ceylon, 1906.12.3.11 and 1936.12.30.63, Thornely Coll.), and *C. areolatum* (Canu & Bassler), (Philippines, 1931.12.30.106, 107, Canu & Bassler Coll.), they consist distally of a pair of large multiporous rosette plates, surrounded by ridges of calcification, similar to those of *C. oranense* and

C. brancoense (see p. 19) ; but in *C. porcellanum* they approach a chambered structure like that of *C. contractum* (see p. 14).

The number of oral spines in *C. contractum* is variable. Four are present in most of the material from west Africa and the Gulf of Mexico. The zooecia of the Galapagos, Kingstown harbour and Mauritius specimens, however, have 5–8 spines ; while Marcus (1937) figured 7 spines in Brazilian, and Norman (1909) 6–7 in Madeiran, material.

Whereas colonies from the Cape Verde Islands, Senegal and the Bay of Biafra encrust stones and shells, those from the coast of Ghana almost exclusively encrust the Foraminiferan *Jullienella foetida* (see p. 8). Distribution. Madeira, Cape Verde Islands, west Africa, Brazil, West Indies, Tortugas, Florida, Long Island Sound, Woods Hole, Panama, California, Colombia, Galapagos.

13. ***Cleidochasma oranense*** (Waters)

(Pl. 2, fig. 3, Pl. 3, fig. 2, Text-fig. 6A–B)

Lepralia oranensis Waters, 1918b : 101, pl. 12, figs. 11–13, Oran, " zone coralligène " 54 fath.; Petit Tahou, Liberia. Canu & Bassler, 1928b : 33, pl. 3, figs. 8–10, Cap Blanc, 20–30 m.

Gemelliporella oranensis (Waters) Barroso, 1925 : 177, text-figs. 1, 2, Oran, 62–65 " brazas " (= fathoms).

LECTOTYPE, chosen here, Manchester Museum, slide from Oran, 54 fath., Waters Collection.

MATERIAL (specimens with ovicells* marked with an asterisk). " *Calypso* " *Coll. I.* Stn. 1, 21° 05′ N, 17° 14′ W, 10.v.56, 43–45 m., C51D* (on barnacle), and C52C (on shells and *Schizzamina* sp., a Foraminiferan).

Marche-Marchad Coll. I. Konakrey, Guinée Ise., 1D*, 21*. Sud de Gorée, 24.ii.53, 40–41 m., 11E. Cap Matakong, 4A (on *Pecten* shell, encrusting base and erect branches). S.W. Madeleines, 15.ix.53, 48 m., 25A*, and 9.i.54, 45–46 m., 27C*. Sud de presque l'île de Cap Vert, 18.ii.54, 95 m., 33D.

Coll. II. S.E. des Madeleines, 15.ix.53, 48 m., 2A. Baie de Gorée, 50–100 m., 7G. Large de Gorée, 5.vii.55, 50 m., 8D, 27E. S.W. Cap Manuel, 20.ii.56, 50 m., 13A. Au large de Saloum, 9.iii.55, 50 m., 17C. S. Baie de Gorée, 18.ii.54, 95 m., 30A. S.W. Madeleines, 9.i.54, 47.5 m., 31O* (unilaminar erect expansions), and 15.ix.53, 48 m., 40C*.

Coll. III. Either S.W. Madeleines, 15.ix.53, 48 m., or S. de Gorée, 13.xi.53, 34–37 m., 16A. Large de Gorée, 50 m., Stn. 55.vii.5A, 18C. S.W. Cap Manuel 50 m., Stn. 56.iii.20D, 26A ; and Stn. 56.ii.20B, 25B. " Gérard Fréca " Dragage 1, 18.ii.54, 23D ; Dr. 5, 27B. No information, 21C, 24C.

Achimota Coll. I. Stn. 47, Dredge haul No. 1, 4.i.57, 44 m., 14E. Stn. 62, as above, No. 2, 18.i.51, 30 m., 87IB. Stn. 117, Agassiz trawl No. 2, 5.iv.51, 64 m., 32D, & Coll. II, 13A. Stn. 132, as above, 2.v.51, 44 m., 50A.

Coll. II. 23R, Chorkor shore, seine net, 12.v.50 (worn).

British Museum, Cap Blanco, west Africa, 11–35 fath., 1921.5.23.7 and 1927.10.30.11, Metzelaar Coll. west Africa, 1959.2.16.1.

Manchester Museum. Waters Coll. 5 slides from Oran, the lectotype, labelled

" material sent by Canu ", is probably the specimen figured by Waters on pl. 12, fig. 11. 2 slides from Jullien Coll., Petit Tahou, Liberia.

C. oranense is not present in the "Calypso" Collection II, from the Cape Verde Islands (see p. 20).

DIAGNOSIS. Zoarium with an encrusting base and erect branches composed of superposed layers of zooecia. Zooecia with large marginal pores and occasional small frontal pores. Orifice with 4 oral spines, cleithridiate, with large condyles, proximal edge of anter straight. Operculum globose distally with a pair of lateral sclerites. 2 distal and 1–2 lateral rosette plates. Avicularia large, interzooecial, numerous, directed distally, with an acute rostrum and complete bar. Mandibles long and curved. Ovicells hyperstomial, but immersed, eventually almost hidden by secondary calcification, with a small area on the proximal frontal border. Polypide with 15 tentacles (Barroso).

Dimensions. Lz 0·50 mm., lz 0·30 mm., Lo 0·19 mm., lo 0·13 mm., Lav 0·40 mm., Lm 0·35 mm., Lov 0·20 mm., lov 0·25 mm.

The zoarium of *C. oranense* has an encrusting base, from which grow erect,

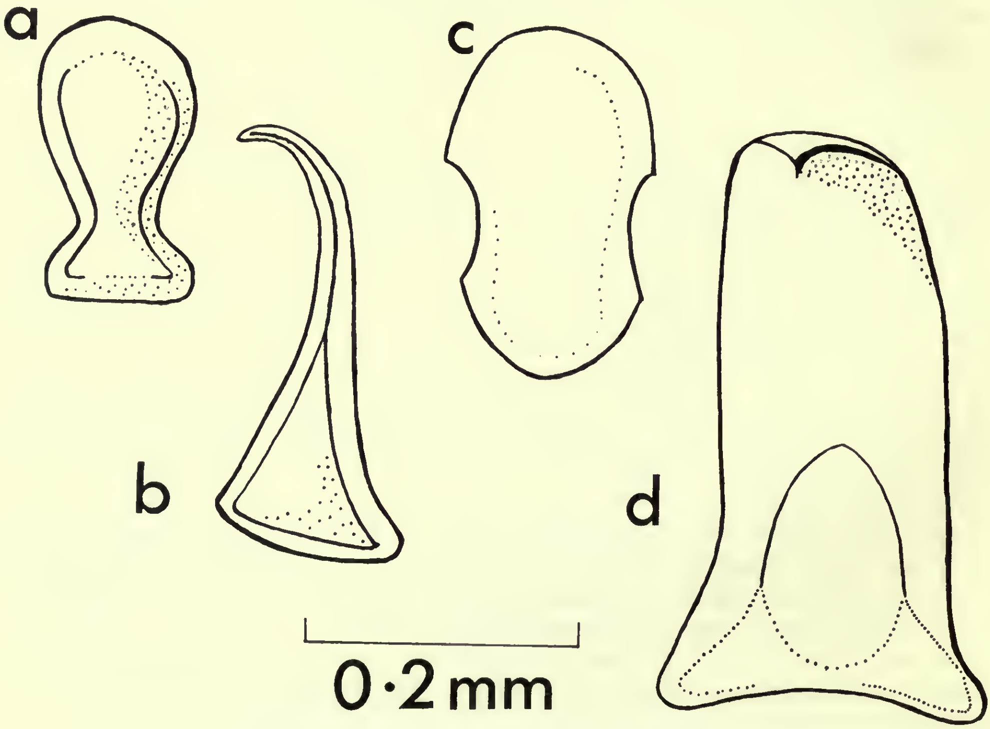

FIG. 6. Opercula and mandibles in *Cleidochasma*. A, B. *C. oranense*. A. Operculum. B. Mandible, Ghana, Achimota Coll., 32D. C. D. *C. brancoense*. C. Operculum, Bay of Biafra, " Calypso " Coll., C55F. D. Mandible, Cape Verde Islands, " Calypso " Coll., C97A².

irregular branches which occasionally anastomose. The colony is frequently large (maximum height observed 60 mm.), and the branches are hollow, or in some cases grow round an algal or hydroid core. The structure of each branch is plurilaminar, secondary layers being budded from the base of the branches ; these usually grow in the same direction as the primary layer (cf. *C. brancoense* below).

The operculum has been figured by Waters and Barroso ; it is semi-globose distally, and usually golden-brown in colour. Barroso also figured the pair of large distal rosette plates. In *C. oranense* the distal wall of each zooecium is concave, and thus the rosette plates are closer together than those of *C. brancoense* (see below).

The avicularian chambers communicate with the neighbouring zooecia by lateral septula, but do not reach the basal wall of the zoarium. Each zooecium usually has an avicularium on one distal-lateral wall, but occasionally it may be absent ; the avicularia seem to arise above the marginal pores, after the zooecial walls have been laid down at the growing edge.

Ovicells do not appear to have been described before in *C. oranense.* When young, they are large, wide and prominent, with a small area on the proximal border. They are rapidly immersed by secondary calcification, and even in slightly older parts of the colony they are inconspicuous, the obscured distal part of the operculum being the only sign of the presence of a fertile orifice, which does not otherwise differ in any way from those of other zooecia (see pl. 2 fig. 3).

C. oranense is known only from the north and west African region, from Oran to the coast of Ghana. It has not been reported from Madeira or the Cape Verde Islands, and is absent from the Bay of Biafra (cf. *C. brancoense* below).

14. ***Cleidochasma brancoense*** (Calvet)

(Pl. 2, fig. 4, Pl. 3, fig. 1, Text-fig. 6C–D)

Lepralia brancoensis Calvet, 1906a : 159 ; 1907 : 410, pl. 27, figs. 6–9, Cape Verde Islands, îlot Branco, 110–180 m. Waters, 1918a : 4 (listed only).

MATERIAL (specimens with ovicells* marked with an asterisk). "*Calypso*" *Coll. I.* Stn. 45, 0° 25′ N, 9° 1′ E, 8.vi.56, 73 m., C55F* (with *C. porcellanum* C55C).

Coll. II. Stn. 24, 15° 16′ 34″ N, 23° 47′ 44″ W, 18.xi.59, 55–60 m., C91I, C94A, C97A*. Stn. 26, 15° 16′ 30″ N, 23° 47′ 31″ W, 18.xi.59, 50–65 m., (île Sao Tiago), C65L*, C127F*. Stn. 31, no details, C66R.

C. brancoense is not present in the Marche-Marched or Achimota Collections.

DIAGNOSIS. Zoarium encrusting with erect, plurilaminar, irregular anastomosing solid branches formed by spiral growth. Zooecia with large marginal and occasional frontal pores. Orifice with 2 oral spines, cleithridiate, with a pair of large condyles forming a subtriangular sinus. Operculum with a pair of lateral sclerites. 2 distal and 1–2 lateral rosette plates. A pair of small rounded avicularia with a complete bar and rounded or triangular mandibles, level with the distal border of the orifice, usually directed inwards and slightly proximally, frequently present, also on the fertile zooecia. Occasional large interzooecial avicularia, with a complete bar and elongated spathulate mandibles present. Ovicells hyperstomial but immersed, becoming obscured by secondary calcification, with a small area on the proximal frontal border.

Dimensions. Lz 0·60 mm., lz 0·45 m., Lo 0·26 mm., lo 0·16 mm., Lop 0·25 mm., lop 0·15 mm., La 0·15 mm., La (interzooecial) 0·50 mm., Lm (interzooecial) 0·40 mm., Lov. 0·25 mm., lov. 0·37 mm.

The zoarium of *C. brancoense* is very similar in appearance to that of *C. oranense*, but differs in the method of growth of the erect branches, which are solid. The secondary layers may arise randomly on the primary layer and develop in any direction from these foci, some branches when broken show a spiral structure similar to that of *Hippoporidra senegambiensis* (Carter) (see p. 25).

The distal wall of each zooecium is convex, with a strong central ridge ; thus the pair of rosette plates are widely separated, unlike those of *C. oranense*.

The large interzooecial avicularia are sporadic in occurrence, often being absent over areas of the colony.

Calvet's material had no ovicells ; those in the " Calypso " specimens are larger and wider than those of *C. oranense*, and are even more rapidly obscured by secondary calcification ; only a few show a small area on the proximal border.

C. oranense and *C. brancoense* are closely related species ; the distribution of *C. brancoense* is confined to two widely separated areas, the Cape Verde Islands and the Bay of Biafra, in neither of which *C. oranense* has been found.

15. ***Cleidochasma rotundorum*** (Norman)

(Pl. 1, fig. 2, Text-fig. 5B, C)

Cellepora janthina (Smitt) Waters, 1899 : 14, pl. 3, figs. 1–3, Madeira (not *Hippoporidra janthina*, see p. 27). Canu & Bassler, 1920 : 615, text-figs. 185A–E.
Cellepora rotundora Norman, 1909 : 311, pl. 42, figs. 8, 9, Madeira, 70 fath.
Hippotrema rotundora (Norman) Canu & Bassler, 1928a : 141.

LECTOTYPE, chosen here, specimen in the Museo do Seminario, Funchal, figured here on pl. 1, fig. 2.

LECTOPARATYPES, remaining specimens on the same slide.

MATERIAL.

British Museum, Madeira, 70 fath., 1911.10.1.1664, Norman Coll.

C. rotundorum is not present in the "Calypso" Collections, the Marche-Marchad Collections or the Achimota Collections.

DIAGNOSIS. Zoarium encrusting, plurilaminar or discoidal. Zooecia with marginal pores and 2–3 rows of frontal pores, the area proximal to the orifice non-porous. 1–2 lateral and 2 distal multiporous rosette plates present. Orifice rounded, with a pair of distinct denticles forming a shallow, rounded sinus ; peristome raised laterally and a small proximal umbo sometimes present. Avicularia adventitious, frequently paired, beside the sinus, directed distally, with a complete bar and triangular mandible. Ovicells prominent, globose, finely and regularly tuberculate, with a very large triangular membranous frontal area.

Dimensions. Lz 0·45 mm., lz 0·30 mm., Lo 0·13 mm., lo 0·13 mm., Lav 0·09 mm., Lov 0·20 mm., lov 0·27 mm.

C. rotundorum somewhat resembles *C. mirabile* Harmer (1957 : 1045, pl. 71, figs. 15, 17, 18, text-fig. 113 ; 600D, Borneo Bank, 59 m.), which also has globose, tuberculate ovicells with large frontal areas, and similar avicularia. *C. rotundorum* differs in the less elongated shape of its orifice and in the absence of oral spines. The zoarium of *C. mirabile* is selenariiform, and the basal surface has characteristic deep depressions (see Harmer, 1957 : 1045). *C. rotundorum* may perhaps assume a selenariiform habit, but the lectotype and the specimens in the Norman Collection are all encrusting. Some colonies in both collections grow over small lamellibranch shells, almost covering both surfaces and thus producing conical, free colonies. These may be those described as " disk-shaped " by Waters. The remainder of the specimens encrust calcareous tubes of the serpulid worm, *Ditrupa arietina*[1] (O. F. Müller).

Waters's figure of the ovicells of *C. rotundorum* shows the extensive frontal areas more clearly than that of Norman, where they are drawn in foreshortened view. Only one ovicell in Norman's Madeiran specimens has the membranous covering in position, in all the others it is no longer present, and in many the ovicell is broken, only the basal wall remaining (see Text-fig. 5C).

The frontal pores are more extensive in this species than in any other *Cleidochasma*, but are not found in the central sub-oral area, which is tuberculate and often umbonate. Waters mentioned the umbo, but both he and Norman illustrated the frontal as uniformly porous. Canu & Bassler (1927 : 21, 31 and 1928a : 141) erected the genus *Hippotrema* for forms with tremopores, including *L. rotundora*, and, as type-species, chose *Lepralia edax* forma *janthina* Smitt (see p. 27), which was also originally figured with a porous frontal. Unfortunately Canu & Bassler did not figure specimens of *Hippotrema janthina*, but referred only to their earlier text-figures of the " *Cellepora janthina* group of Waters " (1920 : 615, text-figs. 185 A–E). These figures are copies of Water's (185A–C) and Norman's (185D–E) illustrations of *C. rotundorum*, not of *H. janthina* (Smitt). Osburn (1952 : 354) pointed out that the frontal of *H. janthina* was not a tremocyst, but that the rows of sub-marginal pores were " carried up " in the calcification to produce an appearance of tremopores. Examples of this type of calcification may also be seen in *Cleidochasma spiculiferum* (Canu & Bassler), which was also originally referred to *Hippotrema* (see below), and in the " cortical zooecia " of *Hippoporidra* (see p. 22).

16. ***Cleidochasma granulosum*** (Canu & Bassler) and ***C. spiculiferum*** (Canu & Bassler)

Hippoporidra and *Cleidochasma* have many characters in common. *Hippoporidra* is here restricted to species with " cortical zooecia " and a special type of interzooecial avicularium, which encrust gastropod shells (see also Lagaaij, 1952 : 147).

Osburn (1952 : 356–7) included *Hippoporidra granulosa* Canu & Bassler (1930a : 43, pl. 8, figs. 1, 2 ; Galapagos, 40 fath.) and *Hippotrema* (?) *spiculifera* Canu & Bassler (1930a : 43, pl. 8, figs. 3–5, Galapagos, 40 fath.) in *Hippoporidra*. Both species have 6 oral spines, a character absent in *Hippoporidra*, and, although

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[1] Notes on the identification of this worm and of another associated Polyzoan, *Bugula ditrupae* Busk, from Madeira, are given by Ryland (1960 : 94–96).

H. granulosa encrusts shell, neither have any association with Gastropod or hermit-crab, nor do they possess cortical zooecia or interzooecial avicularia. Thus neither can be referred to *Hippoporidra* as defined here. Specimens of *H. granulosa* (Galapagos, 40 fath., 1933.12.10.29, " part of type material ", and 1933.12.10.10, Canu & Bassler Coll.) have a pair of small distal rosette plates, an elongate, cleithridiate orifice, with an operculum (like that figured by Osburn, 1952, pl. 42, fig. 14) which greatly resembles that of *Cleidochasma porcellanum*. A specimen of *Hippotrema* (?) *spiculifera* (Galapagos, 40 fath., 1933.12.10.6, Canu & Bassler Coll.) has a pair of distal rosette plates and an orifice very like that of *C. rotundorum*. The numerous ovicells (which were not found by Canu & Bassler) also resemble those of *C. rotundorum* and *C. mirabile*, being large, globose, finely tuberculate, and having a large triangular membranous frontal area. The avicularia are adventitious, and the long curved mandible is directed proximally. Both *H. granulosa* and *H. spiculifera* are here referred to *Cleidochasma*.

17. ***HIPPOPORIDRA*** Canu & Bassler

Hippoporidra Canu & Bassler, 1927 : 21, 31 ; 1929 : 418, text-fig. 163. Lagaaij, 1952 : 147.

TYPE SPECIES, *Cellepora edax* Busk, 1859 : 59, pl. 9, fig. 6 ; pl. 22, fig. 3, Pliocene, Suffolk.

DIAGNOSIS. Zoarium normally encrusting Gastropod shells, frequently (perhaps exclusively) those inhabited by hermit-crabs ; plurilaminar, nodular, branched, massive. Autozooecia with marginal pores and a few frontal pores, and with dietellae. Orifice hippoporine, variable, with a pair of strong denticles. Oral spines absent. Nodules and branches formed by *cortical zooecia*, with 3–4 rows of frontal pores and reduced orifices. Avicularia small, frontal, and small and large *interzooecial*, with triangular and spathulate mandibles. Ovicells hyperstomial, with a frontal area, not closed by the operculum.

Cortical zooecia. Large zooecia (Lz twice that of autozooecia), recumbent in the primary layer, erect in subsequent layers. Frontal apparently pierced by tremopores but in fact, with 2–3 rows of " carried up " pores (see above). Orifices reduced, surrounded by large peristomial tubercles. Polypides not found, zooecial cavity lined by a thick yellow membrane and filled with fibrous and granular material. These cortical zooecia form the base and core of the nodules and branches.

Interzooecial avicularia. Avicularia in which the sub-rostral chamber is very large, with dietellae, and a frontal wall with both marginal and frontal pores. In the primary layer a small avicularium is centrally placed and variously orientated. In the later, superposed layers, where these avicularia form part of nodules or branches, the erect nature of the sub-rostral chamber reduces the extent of the frontal, and the avicularium may appear to be adventitious. The largest avicularia are only found as part of the nodules or branches. The sub-rostral chamber is large and very convex, and the mandibles are very variable in shape. The muscles fill the sub-rostral chamber.

Each species of *Hippoporidra* displays a wide individual range of variability, but some characters seem to be fairly constantly correlated, and it is upon these that specific status is based in the descriptions below. It must however be stressed, that until the breeding and development of living colonies have been observed, together with a full analysis of the association with Gastropod and/or hermit-crab, the separation of the records and specimens below into species, is of necessity arbitrary, and may not reflect actual relationships.

18. NOTES ON THE ASSOCIATION OF GASTROPODS AND PAGURIDS (HERMIT-CRABS) WITH ENCRUSTING ANIMALS

A number of animal species are known to live upon the shells of Gastropods, whether these are inhabited by the Mollusc or by hermit-crabs. Stechow (1921 : 29–31) described two encrusting coelenterates, *Janaria mirabilis* and *Hydrocorella africana*, with branched growths. Specimens of *H. africana* examined (Coelenterate section register, 1957.4.26.22, False Bay, S. Africa), measure 13 mm. across, but have no branches, and are botryoidal. A very fine lamina of the Coelenterate grows out around the orifice of the shell, as in *Hippoporidra* (see p. 25). Growth of a similar lamina was also noted by von Marten (1877 : 183) in an un-named Polyzoan associated with a hermit-crab from South Africa (see p. 32). Hesse & Doflein (1943 : 533, text-fig. 596), described a spiny Coelenterate, *Hydractina sodalis*, encrusting a shell inhabited by *Eupagurus* sp. *H. sodalis* is similar to *Palythoa senegambiensis* Carter (1882 : 418, pl. 16, fig. 2A–C, 3A, B) which has 4 erect arms. Other associations of Coelenterates with hermit-crabs were noted by von Marten (1876 : 20).

Botryoidal colonies of the Ctenostomatous Polyzoan *Alcyonidium nodosum* were described by O'Donoghue & de Watteville (1944 : 428, pl. 16, figs. 17, 18) and O'Donoghue (1957 : 92), encrusting a Gastropod, *Comminella papyracea* from S. Africa. Specimens of *A. nodosum* (1963.3.20.12, Port Nolloth and Lamberts Bay, S. Africa, O'Donoghue Coll.) show that the large zooecia forming the nodules somewhat resemble the cortical zooecia of *Hippoporidra* (see p. 22). They are about twice the length of the autozooecia, and appear to be filled with granular material. Plurilaminar, erect irregular branches are present in *A. polypylum* Marcus (1941 : 63, pl. 8, fig. 27) encrusting *Murex* from Brazil, but the description does not mention groups of enlarged zooecia.

The membraniporan Cheilostome, *Antropora tincta* (Hastings) produces plurilaminar erect branches (up to 50 mm. in length) when encrusting gastropod shells inhabited by hermit-crabs (see Osburn, 1950 : 54, pl. 4, fig. 7 ; pl. 29, figs. 7–8, S. California to Galapagos). The original colonies described by Hastings (1930 : 708) encrust shell fragments and stones, and although plurilaminar, have no erect outgrowths. In *Conopeum commensale* Kirkpatrick and Metzelaar (1922 : 983, pl. 1, fig. 1–9, pl. 2, fig. 14) from west Africa, which is associated with hermit-crabs, the zoarium is plurilaminar without either nodules or erect branches (Cook MS).

Several Polyzoan species, all with branched zoaria and all associated with hermit-crabs, have been recorded from west Africa. Unfortunately their zooecial characters were not described, and although it is very probable that they are synonymous with *Hippoporidra senegambiensis*, *H. picardi* or *H. littoralis* this cannot be established beyond doubt. The records are as follows :—

(a) *Keruniella valdiviae* and *Cellomma keruniformis*, from the mouth of the Congo, associated with *Eupagurus pollicaris* Say var. *alcocki* Balss. ; see Stechow, 1921 : 31 and Doflein, 1914 : 350, text-fig. 302C. Fig. 302D shows *Eupagurus varians* Bened. with a similar branched growth covering the shell inhabited by the hermit-crab.

(b) *Eschara perosa* Kirchenpauer MS, Studer (1889 : 28), on a Mollusc shell. The colony had cylindrical branches and was from a sandy substrate off west Africa (4° 40′ N, 9° 10′ W, with *Cupuladria* sp.). Studer (p. 54) also listed *Eschara* sp. from S. Africa (33° 59′ S, 17° 52′ E, 91·5 m.) growing on *Fusus mandarinus* inhabited by *Eupagurus ungulatus* Studer. This specimen was figured (pl. 23, fig. 8A) with two stout branches, at 180° to one another, extending laterally from the orifice of the shell. It is very similar in appearance to the figure of "*Schizopodrella*" sp., associated with *Pagurus corallinus* given by Schmitt (1931, text-fig. 43), which had in addition a median branch (see p. 25).

Roger & Buge (1948 : 461–470) examined several species of fossil and Recent Polyzoa encrusting shells, by means of X-ray photography. They concluded that in the fossil specimens the association was between Polyzoan and Gastropod, not Polyzoan and hermit-crab. However, Buge (1957 : 320–323), having examined a large number of Recent specimens from west Africa using the same methods, concluded that it was possible that the association was between Polyzoan and Pagurid. He also considered whether the association might be primarily with the Gastropod, and secondarily with the Pagurid, but inclined to the former theory. The lectotype and other specimens of *H. edax* have been examined by means of X-rays. No positive evidence of association with hermit-crabs has been found in the fossil specimens, but of 200 Recent specimens of *H. edax* and *H. senegambiensis* examined 120 were inhabited by hermit-crabs. In young colonies the proportion is even higher ; 41 out of 50 specimens of *H. senegambiensis* (Achimota Coll. 87AI) had hermit-crabs present. In no case has a Mollusc been found, all the remaining shells being apparently empty. A few shells from west Africa examined from the Mollusca Section of the British Museum had no Polyzoan encrustation and were inhabited by the original Gastropod. Thus it appears that the association in Recent species is undoubtedly between Polyzoan and Pagurid.

In the lists of material below, those shells which can be seen to be inhabited by a hermit-crab are marked with an asterisk, thus :—11A*.

19. DEVELOPMENT AND STRUCTURE OF THE ZOARIUM IN *HIPPOPORIDRA*

Some of the larger shells indicate that there may be initial settlement of several larvae and that the final zoarium is formed by the most successful colony ; but, in the great majority of shells, the zoarium appears to be the result of the settlement of a single larva. The following specimens, all of *H. senegambiensis*, are particularly instructive :— Marche-Marched Coll. I, 6D, III, 9A ; Achimota Coll. I, 44I, 87AI, II, 9A. In one case (44I) the ancestrula is visible ; the orifice is rounded, with very little sinus. In all these specimens the colony starts from a point near the orifice of the shell, and, where a hermit-crab is present, above the flexure of the larger chela.

The colony first develops as a unilaminar sheet over the shell, producing cortical zooecia and interzooecial avicularia. Nodules of plurilaminar growth, with cortical zooecia at their centre, and groups of ovicells in the hollows between them, are evident, often before the shell is completely covered by the primary layer of zooecia. Where the shell is of the long-spired *Turritella* type, the first branch is developed early, also before the shell is completely covered ; it is almost invariably at an angle approaching 180° to the long axis of the shell, so that it grows in the direction away from the spire. Subsequent branches tend to develop in a median position in a plane at 90° to the spire of the shell. On short-spired shells or those where several barnacles have also settled, the growth is nearly always nodular and branches are rarely formed, and there seems to be some correlation between shell-type and zoarial form. The erect branches are themselves nodular, with groups of cortical zooecia, and secondary branching occurs in large zoaria. The cortical zooecia apparently form the core of each branch, each group budding further individuals, while the surrounding autozooecia grow up and cover the protuberance thus formed. Sections of branches show the large central cortical zooecia, and the small zooecia of the covering layers, which appear to develop spirally in some zoaria (cf. *Cleidochasma brancoense*, p. 20). Some very large colonies are almost globular, and appear to be the result of plurilaminar growth between the branches, which becomes so thick that they are obscured.

The zoarium is usually extended as a lamina surrounding the shell-orifice and forming a cowl over the carapace of the hermit-crab. This is particularly well-developed in some specimens of *H. picardi* (Marche-Marchad Coll. III, 11A) where the lamina has also developed ventrally to the Pagurid and formed a tube. In one of these zoaria the tube has become so extended that its orifice is apparently too small for the Pagurid to pass through. The pattern of zooecia which is seen on the basal side of the free lamina has led some authors to presume that it marks the position of the original shell orifice and that the shell itself has been eroded by the Polyzoan (see Busk, 1859 : 59, and Carter, 1882 : 417). Both X-ray photographs and broken specimens show that the shell is not eroded and is present even in large colonies, where there is considerable plurilaminar growth. For example, *H. senegambiensis* from Loanda, 1896.7.30.1, is a broken zoarium in which the shell may be seen embedded in from 30–50 layers of zooecia.

The pigmentation of the zoaria of *H. janthina* was noted by Smitt (1873 : 64) and Osburn (1952 : 355). Carter (1882 : 417) described the pigmented areas of *H. senegambiensis* in detail, but examination of the plentiful material now available has shown that their distribution is not constant. Carter found that the cortical zooecia were pigmented and the surrounding depressed fertile areas were not. Zoaria with this type of pigmentation, and also with the reverse arrangement are present in *H. senegambiensis* from the Marche-Marchad Coll. III, 14A. A section through a branch shows that the areas of pigment alternate in position throughout the growth of the colony.

The very large interzooecial avicularia are usually present at the base of the nodules and branches, surrounding the groups of ovicells, which are always found in the hollows between the cortical zooecia, as noted by Carter (1882 : 417). The frontal area is completely membranous in young ovicells of all species, but it rapidly becomes calcified, resulting in a semicircular plate with a small distal, membranous pore.

20. ***Hippoporidra edax*** (Busk)

(Pl. 3, figs. 5–7)

Cellepora edax Busk, 1859 : 59, pl. 9, fig. 6, pl. 22, fig. 3, Pliocene (Gedgravian), Suffolk ; 1861 : 154, pl. 34, figs. 3, 3A, Coast of Devon. Duvergier, 1924 : 46, pl. 6, figs. 5–10, Helvetian, Miocene, France.

Lepralia edax (Busk) Moore, 1937 : 202, on shell containing *Eupagurus cuanensis*, Fleshwick Bay and N. of Kitterland, 18 fath., S.W. coast of the Isle of Man.

Hippoporidra edax (Busk) Lagaaij, 1952 : 147, pl. 15, fig. 13, pl. 16, fig. 6, Pliocene, Netherlands, synonymy. Buge, 1957 : 320, pl. 11, fig. 2, pl. 12, figs. 3–6, Redonian, western France.

LECTOTYPE. B. 1620, B.M. Palaeontology Department.

MATERIAL. *British Museum*, Palaeontology Dept. B. 1620 and D. 60463, Coralline Crag, Pliocene, Britain.

Zoological Dept., Coast of Devon, 1899.7.1.1410, Busk Coll., fig'd Busk, 1861. Guernsey, 1899.7.1.1410A, 1963.4.16.1, Busk Coll. 1887.7.29.49 (chitinous parts). 1911.10.1.1143, Norman Coll. Plymouth, 1899.5.1.1517, Hincks Coll. Scilly, 35 fath., 1963.3.30.273, Harmer Coll. Port Erin, Isle of Man, 1963.12.30.1*, Eggleston Coll.

Sedgwick Museum, Cambridge. C51007–8, Coralline Crag, Orford Castle, Suffolk. C51009–14, Orford. C51015–26, Hall pit, Sudbourne, Suffolk. C35829–33, Gedgrave, Suffolk. C51395, Sudbourne, Suffolk.

H. edax is not present in collections from west Africa.

Diagnosis. Zoarium encrusting Gastropod shells plurilaminar, nodular. Zooecia with marginal and a few frontal pores. Orifice with a fairly wide, rounded sinus. Cortical zooecia with more numerous frontal pores and reduced orifice. Small acuminate and large acute interzooecial avicularia present, with doubly constricted bar. Ovicell with frontal area.

Dimensions. Lz 0·33 mm., Lz (cortical) 0·60 mm., lz 0·30 mm., Lo 0·10 mm., lo 0·08 mm., Lo (cortical) 0·02 mm., lo (cortical) 0·02 mm., Lav 0·10 mm., Lov 0·13 mm., lov 0·14 mm.

Lagaaij gave his reasons (1952 : 140, 148) for regarding *Cellepora parasitica* Michelin, 1847 as a synonym of *H. edax*, rather than of *C. parasitica* Busk, 1859. The dome-shaped zoarium described as *Lepralia edax* by Waters (1885 : 297) from the River Murray Cliffs, Australia, may have belonged to *Conescharellina*. Duvergier (1924 : 46) first noted that the zooecia composing the zoaria of *C. edax* were of two kinds, and he described the irregularly porous frontal of the cortical zooecia. The Recent specimens from S.W. Britain and the Channel Islands have been included here with the Pliocene material which they resemble more than the closely related *H. janthina* and *H. senegambiensis*. The orifices of *H. edax* have a smaller, deeper sinus than those of *H. janthina*, and the interzooecial avicularia are all acuminate, not spathulate, as in *H. senegambiensis*. The zoaria of *H. edax* are also apparently always nodular, without erect branches, although this may be more a function of the type of shell available than a specific character (cf. *H. littoralis* p. 28).

The zoarium of the lectotype is nodular, measuring 15 mm. × 20 mm. The majority of the zooecia are small with few or no frontal pores. The cortical zooecia are considerably larger with small pits indicating frontal pores. Few avicularia are present, but the same types are present in larger numbers in the specimens from Guernsey and Devon. Ovicells are present in the lectotype (cf. Lagaaij, 1952 : 148) ; they are almost hidden on the face of the shell nearly concealed by the slide, but may be seen by tilting the mount. These ovicells are incomplete, the frontal wall no longer being present, but they so greatly resemble broken ovicells of Recent specimens that it is reasonable to assume that they, too, possessed a similar delicate frontal area.

The specimens in the Sedgwick Museum also have broken ovicells, and zoaria from the series C35829–33 show the frontal pores of the cortical zooecia particularly clearly.

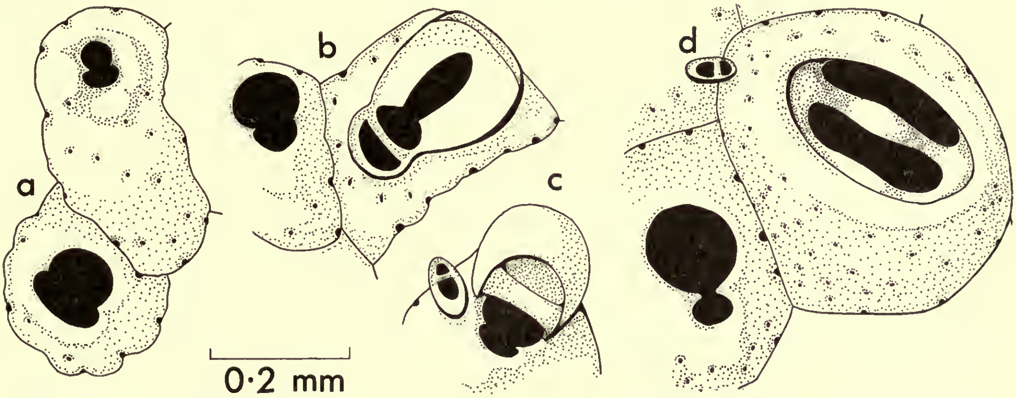

FIG. 7. *Hippoporidra*, treated with eau de javelle. A. *H. littoralis*, zooecium and cortical zooecium, Ghana, Achimota Coll., 7B. B, C. *H. senegambiensis*. B. Zooecium and interzooecial avicularium. C. Ovicell, Ghana, Achimota Coll., 14I. D. *H. picardi*, zooecium and interzooecial avicularium, Senegal, Marche-Marchad Coll. I, 33H.

21. ***Hippoporidra janthina*** (Smitt)

Lepralia edax forma *janthina* Smitt, 1873 : 64, pl. 11, figs. 224, 225, off Florida.

Lepralia maculata Ulrich & Bassler, 1904 : 423, pl. 115, figs. 8a, b, and 9, pl. 118, fig. 7, Calvert Formation, Plum Point, 3 miles S. of Chesapeake Beach, Miocene.

Cellepora minuta Canu & Bassler, 1923 : 182, pl. 25, figs. 10–13, Miocene, N. Carolina, and Pliocene, S. Carolina.

Hippotrema janthina Canu & Bassler, 1928a : 141 (not *Cellepora janthina* Waters = *Cleidochasma rotundorum* see p. 20).

Hippoporidra janthina (Smitt) Osburn, 1952 : 355, pl. 45, figs. 13–15, Gulf of California to Lower California, 2–60 fath.

Hippoporidra edax (Busk) : Soule & Duff, 1957 : 113, Pleistocene, California.

MATERIAL. *British Museum*, Gulf of Mexico, 28° 58′ N., 89° 9′ W., 1961.11.2.14, Cheetham Coll.

H. janthina is not present in the collections from west Africa.

Diagnosis. Zoarium encrusting Gastropod shells, nodular or branched. Zooecia slightly larger than those of *H. edax*, with marginal pores and 2 rows of frontal pores. Orifice with very shallow wide sinus. Small avicularia frequent, larger acuminate avicularia rare. Ovicell wide, with rounded frontal area.

Dimensions. Lz 0·45 mm., lz 0·35 mm., Lo 0·13 mm., lo 0·13 mm.

H. janthina is obviously very closely related to *H. edax*, being distinguished by the wider shallower sinus and the greater frequency of frontal pores. At present, all western Atlantic records are grouped here under *H. janthina*. Soule & Duff stated that *H. edax* had not been " reported as living from the Pacific coast "; there is evidence (Cook MS), that a living form closely related to *H. janthina* has been recorded from Mazatlan, Mexico.

22. ***Hippoporidra littoralis*** sp. n.

(Pl. 1, fig. 3, Text-fig. 7A)

Holotype. B.M. 1963.4.16.3, Achimota Coll. Stn. C.

Material. *Achimota Coll. I.* Stn. C, Winneba shore, rock face, 22.xi.49, 7B,* Paratypes. Stn. U, Tenpobo, No. 1 reef, 21.xi.49, 67F, and *Coll. II*, 4A, 17.i.49. Stn. X, Axim, Hospital reef, 7.i.51, 68E.

British Museum, Malacostraca Section, Apam, Ghana, with *Pseudopagurus granulimanus* (Miers) *biafrensis* (Monod), 1958.5.9.116–7.*

H. littoralis is not present in the " Calypso " or Marche-Marchad Collections.

Diagnosis. Zoarium plurilaminar, nodular. Zooecia with marginal and at most a few scattered frontal pores, frequently with none. Orifice with anter narrower than poster, with a pair of denticles and sub-oral umbo large, constant. Cortical zooecia larger than autozooecia, orifice much smaller, surrounded by large blunt tubercles. Small rounded and semi-circular interzooecial avicularia present, none very large, often extremely rare. Ovicells with frontal area. Inhabits littoral and shallow waters.

Dimensions. Lz 0·28 mm., lz 0·30 mm., Lz (cortical) 0·45 mm., lz (cortical) 0·40 mm., Lo 0·13 mm., lo 0·13 mm., Lo (cortical) 0·07 mm., lo (cortical) 0·05 mm., Lov 0·15 mm., lov 0·18 mm.

It is possible that *H. littoralis* may be found to be a form of *H. senegambiensis* related to growth on short-spired shells (with hermit-crabs), of shallow waters. Until it can be discovered whether the ecological conditions inherent in the Pagurid association are able to affect zooecial as well as zoarial characters, the features in which these specimens differ from *H. senegambiensis* and *H. picardi* must rank as specific. The orifice is constantly wider proximally than distally, even in the cortical zooecia. This is a condition approached by some zooecia of the primary layer in *H. senegambiensis*, but not to the same degree, or so constantly. This type of orifice is also similar to that of *H. janthina*, from which *H. littoralis* differs in the form of the zoarium, the scarcity of frontal pores, and in the type of avicularia present.

H. littoralis is confined to the shore of Ghana. Forest (1956 : 338, text-fig. 2) gave the distribution of the hermit-crab, *Pseudopagurus granulimanus biafrensis* as intertidal, and the association of *H. littoralis* may always be with this and similar littoral species. It may be compared with the deeper water association between *Diogenes ovatus*, *Turritella* shells and *H. senegambiensis.*

23. ***Hippoporidra senegambiensis*** (Carter)

(Pl. 3, figs. 3–4, Text-figs. 7B–C, 8A–D)

Cellepora senegambiensis Carter, 1882 : 416, pl. 16, figs. 1A–V.

LECTOTYPE. Chosen here B.M. 1963.4.16.2A, Guinea, West Africa.[1]

LECTOPARATYPES. 1963.4.16.2B, C.

MATERIAL. *"Calypso" Coll. I.* Stn. 6, 10° 19′ N., 16° 33′ 40″ W., 16.v.56, 73–60 m., C2, specimen 4. Stn. 7, 9° 40′ N, 13° 35′ 5″ W, 12.v.56, 8m., C4C*. Stn. 17, 5° N., 5° 28′ 30″ W., 21.v.56, 27 m., C56H and C36A*, with *Diogenes ovatus* Miors. Stn. 19, 5° 2′ 30″ N., 5° 24′ 40″ W., 21.v.56, 21–27 m., C41A. Stn. 45, 0° 25′ N., 9° E., 8.vi.56, 73 m., C55E.

Marche-Marchad Coll. I. Konakrey, Guinée Ise, II. Baie de Gorée, 1954, 46–48 m., 6D. Sud de Gorée, 24.xi.53, 40–41 m., 11M. A l'est de Gorée, 6.iv.54, 47I*.

Coll. III. " Gerard Freca ", Dragage 1, 18.ii.54, 23J ; 5, 15F ; 7, 8A. Sud de Gorée, 13.xi.53, 33–35 m., 9A* ; 34–37 m., 17A*. Devant l'Anse de Bernard, Dakar, 12 m., 10A*. Baie de Gorée, 14A. Either S.W. Madeleines, 15.ix.53, 48 m., or Sud de Gorée, 13.xi.53, 34–37 m., 17A*. Devant le " Castel ", Gorée, 15 m., 22A*; 33–34 m., 27.xi.53, 29B ; 24K*, no information.

Achimota Coll. I. Stn. K, on trawl debris 1 mile offshore, 2 miles W. of Densu R., 2.iii.49, 4 fath., 44I. Stn. 47, dredge haul No. 1, 4.i.51, 44 m., 14I. Stn. 62, dredge haul No. 2, 18.i.51, 30 m., 87IA*. Stn. 63, as above, 36 m., 87IIA. Stn. 71, as above, 24.i.51, 30 m., 73A*. Stn. 98, as above, 14.iii.51, 25 m., 3B*. Stn. 112, Agassiz trawl No. 3, 4.iv.51, 43 m., 60S and Coll. II, 10A*. Stn. 130, Agassiz trawl, No. 2, 26.iv.51, 32 m., 70B* and Coll. II, 9A*. Stn. 131, as above, No. 1, 2.v.51, 37 m., 43U. Stn. 132, as above No., 44 m., 50F.

Coll. II. Stn. 133, as above, No. 3, 51 m., 7G. Stn. 117, as above, No. 2, 5.iv.51, 64 m., 13F. Stn. 126, as above, No. 3, 12.iv.51, 16 m., 11A (W).

Forest Coll. No. 3*, M'Bizi, Stn. 26, 1948–49, avec *Eupagurus alcocki* Balss (W). No. 4, Dakar, iv.1951. No. 5*, devant Joal, Senegal, 25 m., with *Diogenes ovatus* Miors. No. 6*, Baie de Rufisque, Gorée, 18.i.52, 10–15 m., with *D. ovatus* and *Paguriste fagei* Fort. No. 7*, Entre Rufisque et Gorée, 26.iii.53, 25 m., with *D. ovatus.*

British Museum, Guinea, west Africa, 1963.4.16.2. Guinea coast, 1904.7.16.1, 2, 3, 4 (W). Cape Blanco, 1922.9.12.1*. Loanda, Angola, S. of da Costa, 1896.7.30.1 (W). Locality ? 1851.11.14.82, Belcher Coll.

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[1] Carter (p. 419) gave the location of his specimens as " Liverpool Free Public Museum ". Mrs. N. McMillan, of the City of Liverpool Museums, informs me (*in litt.* 29.7.1963) that " they must be presumed lost in the bombing ". The specimens in box 1963.4.16.2 were labelled as " Type specimens of *Cellepora senegambiensis* Carter " by Kirkpatrick, but none of them is that figured on pl. 16, fig. 1, by Carter.

Diagnosis. Zoarium usually with long branched rugose arms. Zooecia small, with marginal pores and a few scattered frontal pores. Orifices of primary layer with a wide shallow sinus, orifices of subsequent layers usually with a rounder, deeper sinus. Cortical zooecia large, with 3–4 rows frontal pores, and very small orifices with large peristomial tubercles. Small adventitious avicularia frequent, large and small interzooecial avicularia with triangular and spathulate mandibles. Ovicells with frontal area, occasionally tuberculate.

Dimensions. Lz 0·30 mm., lz 0·25 mm., Lz (cortical) 0·70 mm., lz (cortical) 0·50 mm., Lo 0·10 mm., lz 0·10 mm., Lo (cortical) 0·08 mm., lo (cortical) 0·05 mm., Lm 0·04–0·15 mm., Lov 0·11 mm., lov 0·15 mm.

The orifices of the zooecia of the primary layer differ from those later zooecia in that their sinuses are wide and shallow, like those of *H. janthina*. They are never as wide as those of *H. littoralis*, but in a few colonies the primary type persists in a large number of the zooecia which form the plurilaminar branches. These zoaria are also marked by the predominance of the triangular type of inter zooecial avicularium and are labelled " W " in the lists of material above. Colonies of *Hippoporidra* sp. from Fiji (1862.2.4.13) and the Philippines (1882.7.29.48 and 1899.7.1.3518, 3519) also have orifices with a wide sinus and avicularia with triangular mandibles, which are, however, much shorter.

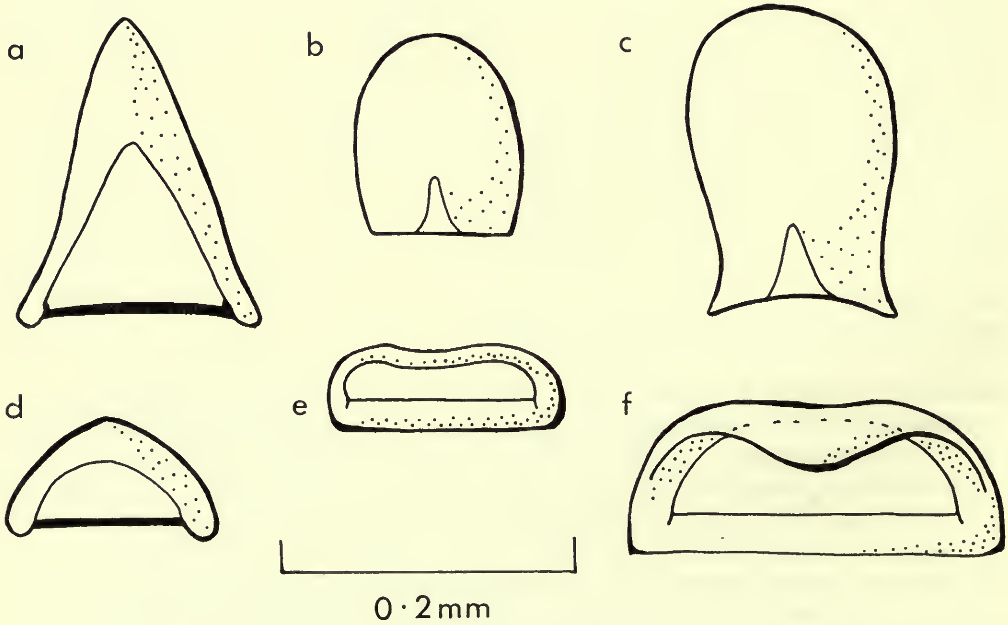

Fig. 8. Mandibles in *Hippoporidra*. a–d. *H. senegambiensis*. a. Acute form, Senegal, Forest Coll. No. 3. b, c. Spathulate forms, Ghana, Achimota Coll. 14I. d. Rounded form, Ghana, Achimota Coll. 14I. e–f. *H. picardi*. e. Small sinuate form. f. Large, beaked sinuate form, Senegal, Marche-Marchad Coll. I, 33H.

The structure of the zoarium has been described above (p. 24). In a few cases the branched arms are not developed (Cape Blanco, 1922.9.12.1 and Forest Coll. No. 6), but in each of these, there has been a heavy settlement of barnacles upon the shell during the development of the Polyzoan.

The large interzooecial avicularia show a great deal of variation. The principal types are spathulate, semicircular and triangular, but there is some intergradation between these shapes. The young ovicell has a large membranous area frontally. Calcification reduces this first with a bar proximally above the orifice, and finally by progressive closure to a small circular distal area. In some zoaria the ectooecium is raised into tubercles distally and laterally, but generally the ovicell is smooth.

H. senegambiensis is distributed round the west African coast from northern Senegal to the Bay of Biafra, and has been found off the coast of Angola. It has not been reported from Madeira, or the Canary or Cape Verde Islands. In character *H. senegambiensis* is intermediate between, but distinct from, both *H. littoralis* and *H. picardi*. The great majority of the colonies are associated with shells of *Turritella annulata* Kiener, which are inhabited by the Pagurid *Diogenes ovatus*. *T. annulata* is found off the Ghana coast from 10–64 m., and is the dominant species of the silty-sand community or *Turritella* zone (see Bassindale, 1961 : 492, 500), which extends from 14·5–36 m. in depth. *D. ovatus* has a bathymetric distribution of 12–40 m. (see Forest, 1956 : 338, text-fig. 2).

24. ***Hippoporidra picardi*** Gautier

(Text-figs. 7D, 8E–F)

Hippoporidra picardi Gautier 1962: 254, text-fig. 22, Gulf of Salonika, Agean Sea, 80–100m.

MATERIAL. *" Calypso " Coll. I.* Stn. 1, 21° 05′ N., 17° 14′ W., 10.v.56, 45–43 m., C1F. Stn. 6, 10° 19′ N., 16° 33′ 40″ W., 16.v.56, 76–60 m., C2A, specimens 1, 2* and 3.

Marche-Marchad Coll. I. Sud de presque l'île de Cap Vert, 18.ii.54, 95 m., 30D and 33H.

Coll. III. As above, 46–50 m., 1A*. Baie de Gorée, 4A. 5610, IBC, 176–200 m., 6A*. Port Etienne, Mauritanie, vii.1953, 37–38 m., 7A. Au large de Gorée, Stn. 556, 95 m., 11A*. " Gerard Freca ", 2–15, 160–140 m., 12A ; N.W. Parar des Almadies, 170–145 m., 13A ; Dragage 5, 18.ii.54, 19A ; 4, as above, 97–98 m., 28B.

Forest Coll. Sud de Gorée, 25.iii.54, 95 m., No. 1*, with *Dardanus arrosor* (Herbst) and *Pagurus cuanensis* Thompson, No. 2.

British Museum, Cape of Good Hope, 1842.12.2.29, Belcher Coll.

H. picardi does not occur in the Achimota Collection.

DIAGNOSIS. Zoarium like that of *H. senegambiensis*. Zooecia larger and more recumbent. Frontal of autozooecia with 2–4 rows of pores. Orifice large, with well-developed denticles and a very small, rounded sinus. Orifices of cortical zooecia reduced in size. Interzooecial avicularia with triangular, spathulate and sinuate mandibles, some very large. Ovicell large with a rounded frontal area.

Dimensions. Lz 0·45 mm., lz 0·30 mm., Lz (cortical) 0·70 mm., lz (cortical) 0·50 mm., Lo 0·14 mm., lo 0·11 mm., Lo (cortical) 0·10 mm., lo (cortical) 0·06 mm., Lm 0·04–0·15 mm., lm 0·05–0·25 mm., Lov 0·20 mm., lov 0·20 mm.

H. picardi differs from both *H. senegambiensis* and *H. littoralis* in its larger zooecia, with more porous frontal, and in the shape of the orifice. The largest interzooecial avicularia, although closely related to those of *H. senegambiensis* with a rounded mandible, differ in their sinuous distal edge (see Text-figs. 8E–F). The ovicells, however, show no significant differences, except their generally larger size. Von Marten (1877 : 183) mentioned a Polyzoan with erect arms growing on a shell inhabited by a hermit-crab from 50 fath. off the South African coast (33° 59′ S., 17° 52′ E.), but did not give any further description. *H. picardi* is now known from the more northerly west African localities, and from the Cape of Good Hope. It is a deep-water form, and it is interesting that the first, and only previous record, is not from the Mediterranean proper, where *Hippoporidra* does not occur (see Gautier, 1962 : 255), but from deep water in the Aegean. Gautier did not give the name of the hermit-crab associated with his specimen. The two species of crab named in the Forest Collection both extend in distribution to a depth of 100 m. *P. cuanensis* has the more northerly range, extending to the south coasts of Britain and Ireland.

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26. SUMMARY

The synonymies of three genera, *Hippoporina*, *Hippoporella* and *Cleidochasma*' are given. Four species of *Hippoporina* are described ; *H. pertusa*, here found from Ghana, has a very wide geographical distribution ; *H. americana*, also widely distributed, is here recorded solely from waters of low salinity in Nigeria. *H. lacrimosa* and *H. acuta*, spp. n., are forms in which the avicularia differ from those of species previously described. *Hippoporella gorgonensis* is recorded for the first time from the eastern Atlantic, and is briefly compared with *H. multidentata*, a species from the Pacific and Indian Oceans. *H. pusilla*, here occurring in the eastern Atlantic from Madeira and the Cape Verde Islands only, is also described. Five species of *Cleidochasma* are described. *C. porcellanum*, which exhibits great variation in the character of the orifice, is a circum-tropical species, here considered to include *C. bassleri* ; *C. contractum*, another widely distributed species, is tolerant of colder waters. Ovicells are described for the first time in *C. oranense* and *C. brancoense*, species with large, erect zoaria. *C. rotundorum* has not been reported from west

Africa, but is found at Madeira, and has been previously confused with one of the species here included in the genus *Hippoporidra*. *Hippoporidra* is re-defined, and two species previously assigned to it, *H. granulosa* and *H. spiculifera*, are referred to *Cleidochasma*. Some associations between Pagurids, Gastropods, and encrusting organisms are briefly listed and the characters peculiar to the *Hippoporidra*-association described. Detailed examination, including X-ray photography, of the large amount of material available, has shown that the Gastropod shell is not eroded by the Polyzoan, and that the Mollusc is absent, so that the association, in Recent specimens at least, is between Polyzoan and Pagurid. *H. edax* and *H. janthina*, neither of which is west African, are briefly defined and described. The occurrence of the three west African species of *Hippoporidra* appears to be correlated with the species of Gastropod shell available, and with the bathymetrical distribution of the Pagurids with which these are associated. *H. littoralis* is an intertidal and shallow-water species, *H. senegambiensis* occurs in deeper waters, and *H. picardi*, which has been previously reported only from the Aegean, inhabits even greater depths, up to 200 m.

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PLATE 1

Hippoporella, *Cleidochasma* and *Hippoporidra*

FIG. 1. *Hippoporella gorgonensis* Hastings. Ghana, Achimota Coll., 36G. Zooecia, those in the centre of the colony with ovicells. ×32.

FIG. 2. *Cleidochasma rotundorum* (Norman). Madeira, Museo do Seminario, Funchal, lectotype. Zooecia with ovicells. ×32.

FIG. 3. *Hippoporidra littoralis* n. sp. Ghana, Achimota Coll., 7B. Zooecia, treated with eau de javelle. ×36.

FIG. 4. *Cleidochasma porcellanum* (Busk). Tortugas, Naturhistoriska Riksmuseet, Smitt Coll., No. 284. (? type of *Lepralia cleidostoma* Smitt). Zooecia and ovicells (see also Pl. 2, fig. 1). ×50.

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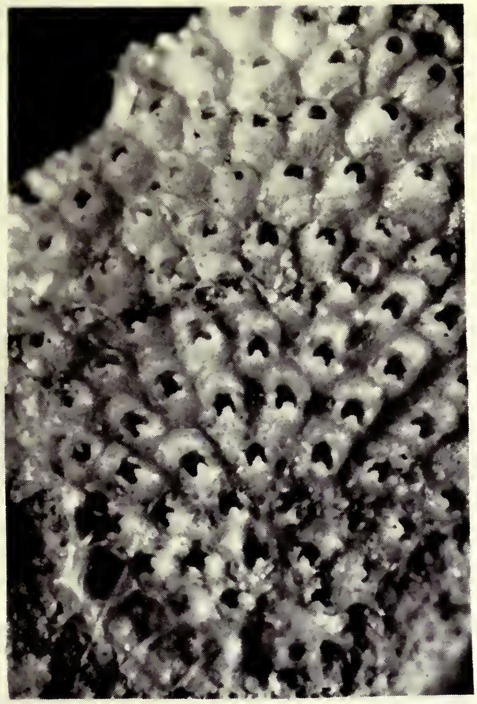

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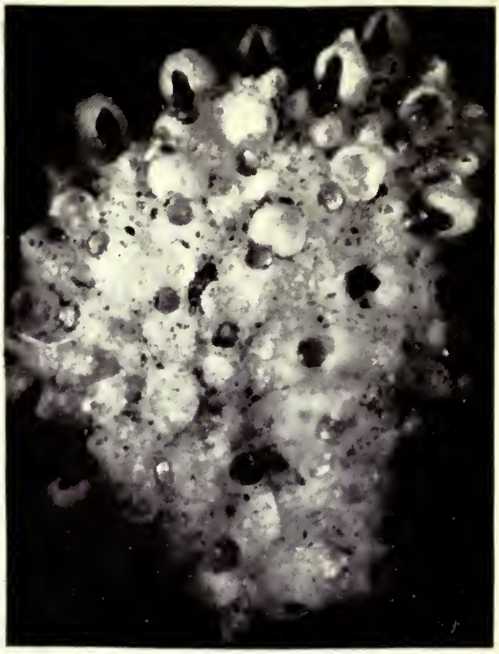

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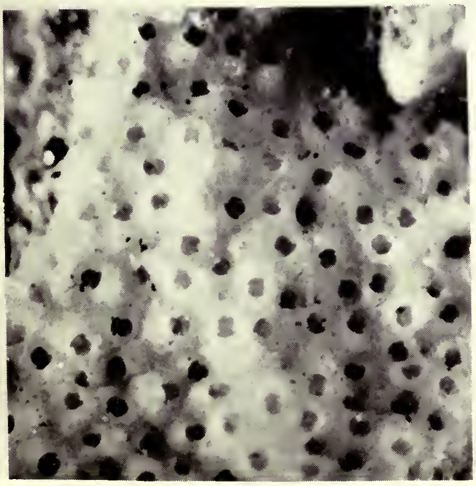

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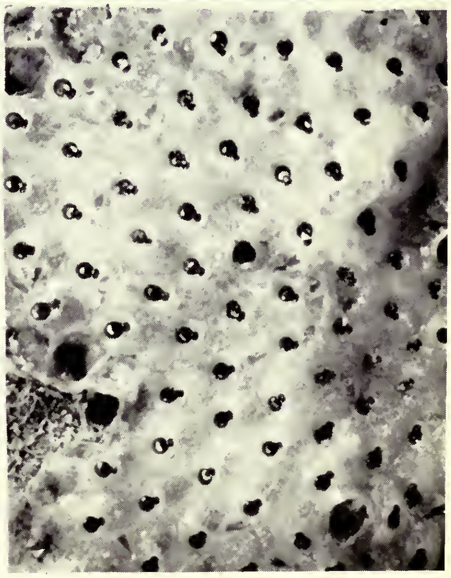

PLATE 2

Ovicells in *Cleidochasma*

FIG. 1. *C. porcellanum* (Busk). Tortugas, Naturhistoriska Riksmuseet, Smitt Coll., No. 284. Striated ovicell (see also Pl. 1, fig. 4). ×113.

FIG. 2. *C. porcellanum*. Ceylon, 1936.12.30.34A pt., Thornely Coll. Zooecia and ovicells with secondary calcification. ×54.

FIG. 3. *C. oranense* (Waters). west Africa, 1921.5.23.7. Zooecia, avicularia and ovicell (*o**). ×54.

FIG. 4. *C. brancoense* (Calvet). Bay of Biafra, "Calypso" Coll., C55F. Ovicell (*o**). ×60.

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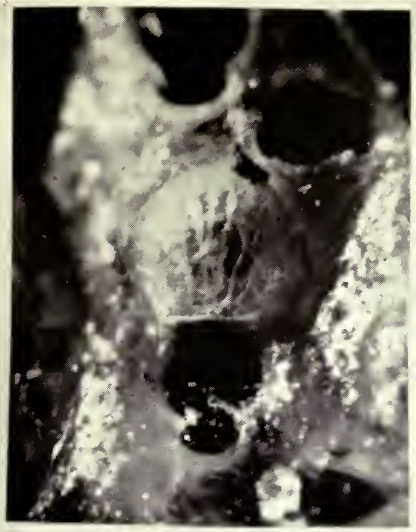

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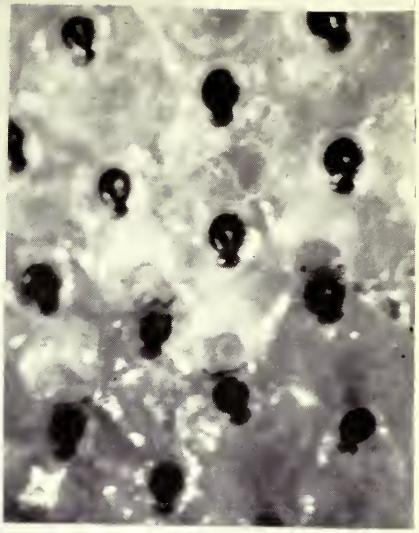

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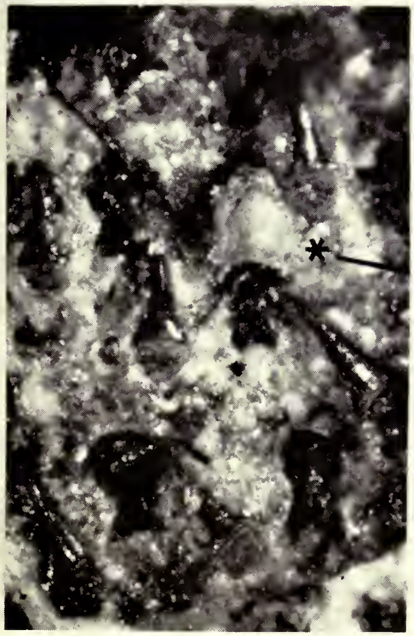

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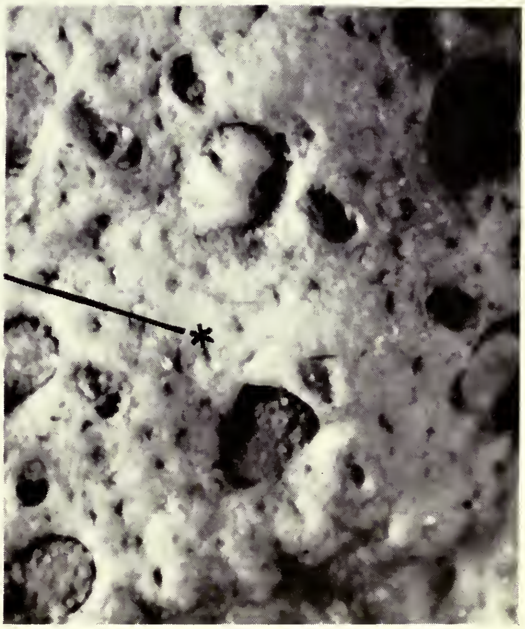

PLATE 3

Cleidochasma and *Hippoporidra*

Fig. 1. *Cleidochasma brancoense* (Calvet). Cape Verde Islands, " Calypso " Coll., C97A. Part of a branch, showing the large interzooecial avicularia ; treated with eau de javelle. × 4.2.

Fig. 2. *C. oranense* (Waters). Ghana, Achimota Coll., 32D. Part of a branch, treated with eau de javelle. × 8.5.

Figs. 3–4. X-ray photographs of *Hippoporidra senegambiensis* (Carter), 5ma, 40KV, 120 seconds.

Fig. 3. Senegal, Marche-Marchad Coll. III, 10A. Showing position of gastropod shell (*s*) and chela of hermit-crab (*c*). × 1.7.

Fig. 4. Guinea, west Africa, 1963.4.16.2 B, C, Lectoparatypes. Showing laminae of Polyzoan growing out from orifice of gastropod shells (*l*). × 1.7.

Figs. 5–7. X-ray photographs of *H. edax* (Busk), 5ma, 40KV, 120 seconds.

Fig. 5. Guernsey, 1963.4.16.1, Busk Coll. × 1.7.

Fig. 6. Plymouth, 1899.5.1.1517, Hincks Coll. × 1.7.

Fig. 7. Britain, Pliocene, Coralline Crag, B1620, lectotype. × 1.5.

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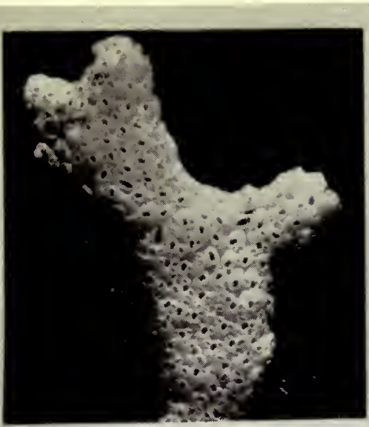

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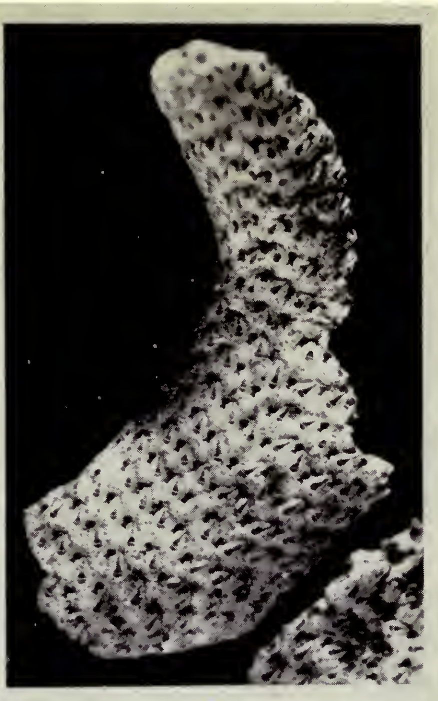

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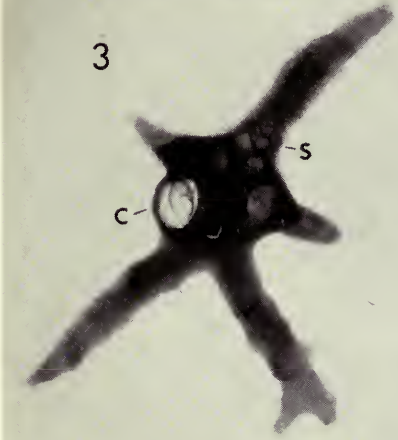

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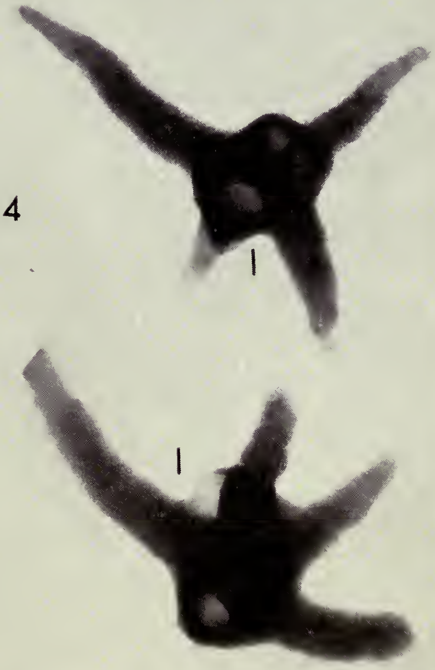

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FRESHWATER GASTROPOD MOLLUSCA FROM ETHIOPIA

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D. S. BROWN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 12 No. 2
LONDON: 1965

FRESHWATER GASTROPOD MOLLUSCA FROM ETHIOPIA

BRITISH MUSEUM
1 APR 1965
NATURAL HISTORY

BY

D. S. BROWN

Medical Research Council, c/o Section of Experimental Taxonomy,
Zoology Department, British Museum (Natural History)

Pp. 37–94 ; *Plates* 1–3 ; 47 *Text-figures*

BULLETIN OF
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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical Series.*

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TRUSTEES OF
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Issued April, 1965 *Price Twenty-one Shillings*

FRESHWATER GASTROPOD MOLLUSCA FROM ETHIOPIA

By D. S. BROWN

SYNOPSIS

Gastropod molluscs were collected by the author between May and September 1962 from a variety of freshwater habitats in Ethiopia. Twenty-eight forms are represented in the collection of which a total of eleven have not been previously recorded from Ethiopia or have been recorded with doubt by previous authors. Two forms in each of the genera *Bulinus* and *Ancylus* appear to be new. It is considered that seven of the forms recorded from Ethiopia for the first time belong to the African component in the fauna, whereas only three are possibly of palaearctic origin. It is concluded that the wide distribution and diversity of some of the palaearctic forms justify the importance attached by Bacci (1951) to the palaearctic element in the molluscan fauna of the Ethiopian Plateau.

INTRODUCTION

A COLLECTION of freshwater molluscs was made by the author between May and September 1962 in the course of a survey to determine the distribution of potential intermediate hosts of human schistosomiasis in Ethiopia. Facilities provided by the Haile Selassie I, University College of Addis Ababa made it possible to visit many regions of Ethiopia, and a wide variety of aquatic habitats between sea level and 3,000 metres (10,000 ft.) were examined. An account of the Gastropoda collected during the survey is given in the present paper. Four new forms of Basommatophora are described and a total of ten do not appear to have been previously recorded from Ethiopa. Prosobranchia are relatively poorly represented in the collection ; no specimens of the genera *Cleopatra, Gabbia* or *Lanistes* were found. This can be only partly attributed to the high altitudes at which most of the work was carried out (over 1,500 m.), as the latter genus is present in Lake Tana (1,900 m.).

The arrangement of families and subfamilies is that employed by Wenz and Zilch[1]. As taxonomy within several families of African freshwater molluscs is in a state of flux at the level of the genus and below, a generic arrangement has been selected from existing accounts of the African fauna. Genera are used in the manner of Mandahl-Barth (1954), and *Bulinus* and *Biomphalaria* are classified in accordance with the species-group system proposed by this author (1957a, b). *Ferrissia* Walker is used in accordance with past practice although according to Dr. B. Hubendick (in litt.) true *Ferrissia* do not occur in Africa. Identifications have been based on shell and anatomy, and information is given that is relevant in comparison to existing descriptions which are amplified in some cases. Wherever possible, the forms in the present collection have been assigned to previously described taxa and where there are differences to the descriptions of previous authors these are discussed. Two forms of *Bulinus*, and one form of *Ancylus* are apparently new but have not been named as it is evident that revision is necessary throughout these genera before the status of these Ethiopian forms can be properly established. One purpose of the present paper is to bring the material to the attention of malacologists who may undertake works of revision in the future.

---

[1] Wenz, W. Handbuch der Palaeozoologie, Berlin. 6. Gastropoda Pt. 1 Prosobranchia 1938–1944. Pt. 2. Euthyneura (by A. Zilch) 1959–1960.

In comparison to other parts of Africa a relatively large number of travellers have made collections of molluscs in Ethiopia. Bacci (1951) gives a comprehensive catalogue of records of Ethiopian Mollusca up to 1941 and proposes many cases of synonymy. Synonymies given in the present paper are primarily local and the references included represent either original locality records or nomenclatural variations. Works in which names have been cited without change are omitted.

Localities are defined in relation to towns or other landmarks which are all listed at the end of the paper with map references. In the text localities are grouped into provincial areas in order to make possible a rapid assessment of distribution by reference to Map 1 in which approximate provincial boundaries are shown. The routes followed during the survey are also indicated on the map. The majority of habitats in which molluscs were found were situated on the Ethiopian plateau between altitudes of approximately 1,800 m. (6,000 ft.) and 2,700 m. (9,000 ft.). A general account of the geography and climate of the country is given by Ayad (1956) ; the distribution and nature of aquatic habitats is described elsewhere (Brown, in preparation). The number of specimens obtained in each sample is shown between brackets, and an asterisk indicates that only empty shells were found.

The collection is deposited in the Section of Experimental Taxonomy, British Museum (Natural History). Specimens have also been deposited in the World Health Organisation Snail Identification Centre, Charlottenlund, Denmark. These collections are referred to in the text as (B.M.N.H.) and (W.H.O.) respectively.

It is a pleasure to record my thanks to Mr. J. MacFarlane and Dr. A. Tjønneland (Haile Selassie I University College, Addis Ababa) for their ready assistance. I am grateful to the Trustees of the British Museum (Natural History) for the provision of working facilities, and to Dr. C. A. Wright for accommodation in the Section of Experimental Taxonomy. Dr. G. Mandahl-Barth has been generous of his time, I am indebted to him for much stimulating discussion and the opportunity to examine the collection of the World Health Organisation Snail Identification Centre. Dr. J. Burch has kindly allowed me to quote some of his unpublished observations on the chromosomes of *Bulinus*. Thanks are due to Mr. D. Claugher and Miss J. Lines for the care they have devoted to the preparation of photographs and radulae.

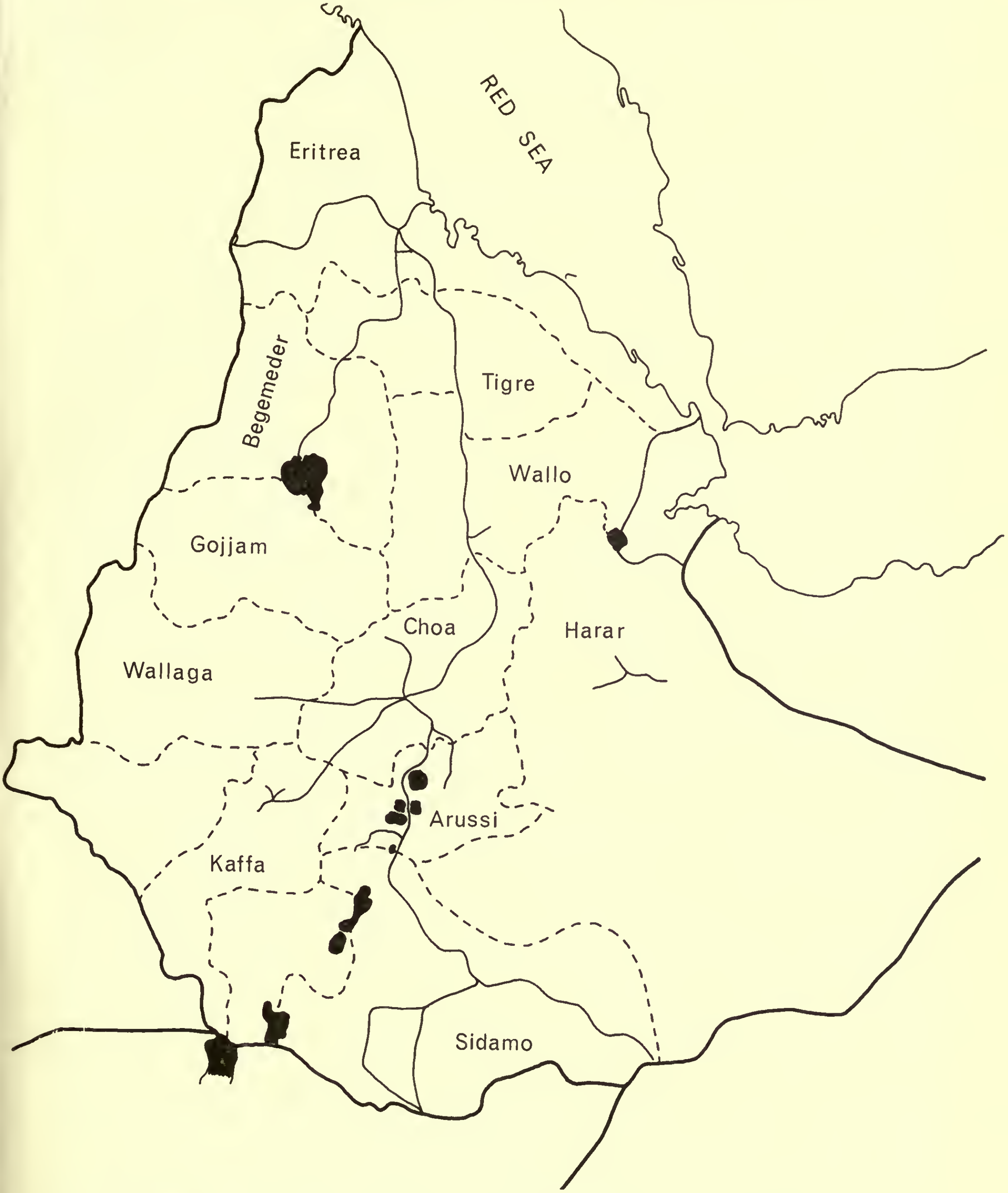
Family **VIVIPARIDAE**

BELLAMYA Jousseaume

Bellamya unicolor (Olivier)

Cyclostoma unicolor Olivier, 1804 : 39, pl. 31, fig. 9 ; *Paludina unicolor* Martens, 1866 & 1867 ; *Vivipara unicolor* ; Jickeli, 1874 ; *Viviparus unicolor ;* Thiele, 1933 ; Bacci, 1940 ; Piersanti, 1940 ; *Viviparus* (*Bellamya*) *unicolor ;* Bacci, 1943 ; *Bellamya unicolor unicolor ;* Bacci, 1951 ; *Bellamya unicolor ;* Mandahl-Barth in Ayad, 1956.

Paludina abyssinica Martens, 1866 : 97, pl. 3, fig. 7, & 1867 ; *Vivipara abyssinica ;* Jickeli


RED SEA
Eritrea
Begemeder
Tigre
Wallo
Gojjam
Choa
Harar
Wallaga
Arussi
Kaffa
Sidamo

Map 1. Ethiopia. Boundaries of Provinces indicated by broken lines ; routes followed in making the present collection indicated by solid lines.

1874 ; *Viviparus unicolor abyssinicus ;* Piersanti, 1940 ; *Bellamya unicolor abyssinica;* Bacci, 1951.

LOCALITIES. Arussi : 5 km. approx. S. of Adamitullo (between Lake Zwai and Bulbulla River) (8)*; Lake Abyata, east shore (1)*. Begemeder : Lake Tana at Gorgora (130).

Shell

Lake Tana (pl. 1, 1 & 2). Although the apices are eroded in the larger specimens many shells are moderately short spired having the length of the spire approximately equal to that of the aperture. The peripheral angulation is acute in young specimens, but is indistinct in large shells. The shoulder angulation is scarcely visible in both big and little specimens. Microsculpture on the apical whorls consists of coarse spiral ridges, which subsequently become finer and wavy and are crossed by irregular transverse growth ridges. In a representative shell there are 5 spiral ridges at the beginning of the second whorl, and 16 at the beginning of the third whorl.

The outer lip of the aperture is thickened and coloured black-brown in many of the larger shells, in others this dark band is present a short distance from the outer lip and further back there may be one or two more according to the size of the shell. All the bands are usually situated in the ultimate whorl. Similar bands have been observed in *Bellamya* from other parts of Africa and it is likely that growth takes place in several stages in such populations.

There appears to be sexual dimorphism in size : 19 of 23 specimens of more than 20 mm. length are female ; 3 of 11 specimens between 15 and 20 mm. are female.

Largest shell : L = 27·7 mm.; ML = 13·7 mm.; W = 19·4 mm.

Arussi : near Lake Zwai (pl. 1, 3). All the shells are distinguishable from Lake Tana specimens of the same size by the more acute peripheral and shoulder angulations, and the relatively sharp apices. Microsculpture on the lower whorls is similar to that of the Lake Tana specimens, but the apical whorls are smooth, probably as a result of weathering. Sub-fossil in a lacustrine deposit.

Largest shell : L = 21·5 mm. ; ML = 10·3 mm. ; W = 16·5 mm. ; 6¼ whorls.

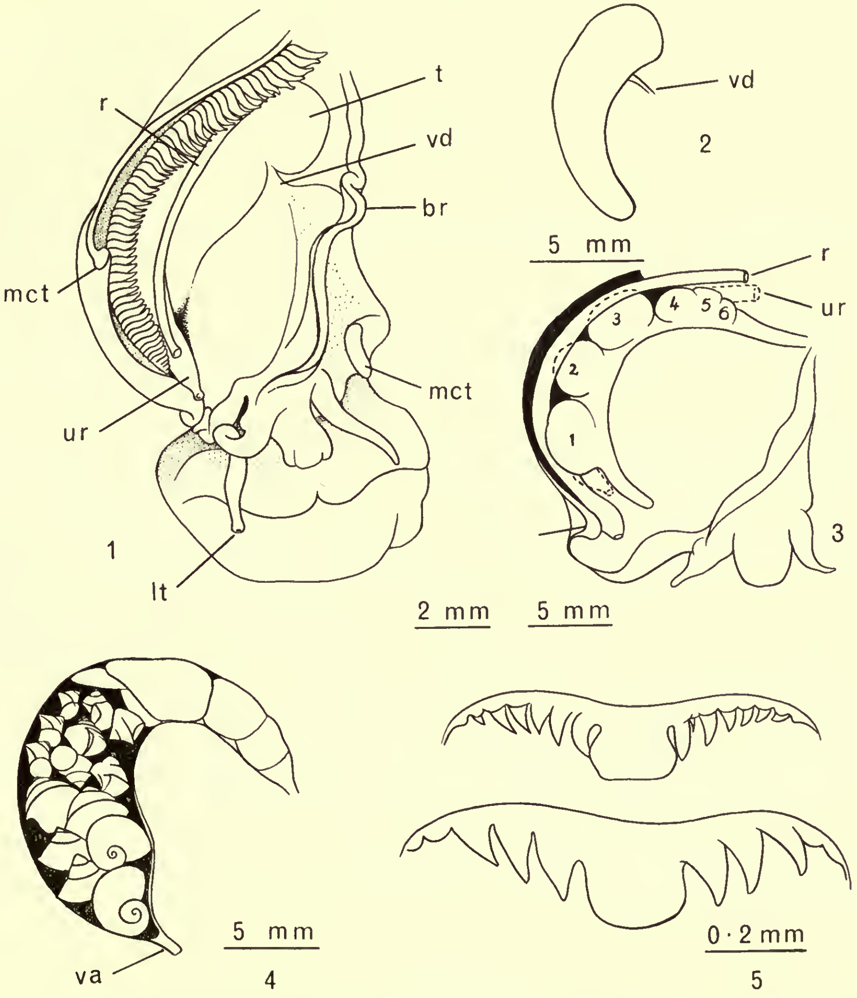
Anatomy (Text-figs. 1–5)

The male genital system (Text-figs. 1 and 2) closely resembles that of *Viviparus* (= *Bellamya*) *unicolor* as described by Rohrbach (1937). A crescentic testis with a narrower anterior end is situated on the right side of the roof of the mantle cavity close to the right side of the rectum. The ureter is attached to the adjoining edges of the testis and the rectum. After emerging from near the posterior end of the testis, the vas deferens passes beneath connective tissue across the floor of the mantle cavity to the left side, where it widens and runs forward beneath a branchial fold as the prostate " gland ". After becoming narrower the vas deferens passes into the right tentacle, at the tip of which is the male aperture.

The uterus occupies a similar position to the testis in the male, with the vagina projecting as a short tube from the floor of the mantle cavity. Great variation was observed in the number and the size of the shelled embryos present in large females of approximately the same size. Occasionally only a single young snail was present’ but more frequently a few large ones were arranged in a single row (Text-fig. 3). In some specimens many young snails were arranged in two or three rows ; the greatest number of young observed in such a uterus being 28 (Text-fig. 4).

Radula (Text-fig. 5)

The length of the median cusp of the central tooth is more than half the breadth of the cusp. There are 3–7 lateral cusps on each side of the median cusp, and in addition the upper lateral edges of the central tooth may bear a few notches.



Figs. 1–5. *Bellamya unicolor* from Lake Tana. Fig. 1. Mantle cavity of male exposed by turning mantle to right. Fig. 2. Testis. Fig. 3. Female of shell length 27·2 mm., left side of mantle removed and the remainder turned to the right exposing uterus, embryos numbered 1–6. Fig. 4. Uterus of female 21·5 mm. shell length with wall removed to expose young snails and embryos. Fig. 5. Cusp bearing parts of two representative central teeth from radula.

REMARKS. In the shape of the shell, and the presence of a short median cusp on the central tooth of the radula, these specimens conform to the *Bellamya unicolor* group described in Uganda by Mandahl-Barth (1954). If the apices were not eroded some of the larger shells from Lake Tana (pl. 1, 1) would approach the elongated shape of *B. abyssinicus* (Martens) in which the spire is approximately equal to 1½ times the aperture length. In addition to the original specimens from South Ethiopia, von Martens' species appears to be known only from Lake Tana (Martens, 1867 and Piersanti, 1940), but the range of variation in the present sample from this lake indicates that the form is not separable from *B. unicolor*.

As appears to be the case in other parts of Africa, *Bellamya* has only been found in or near large bodies of water in Ethiopia. The sub-fossil shells from the vicinity of Lake Zwai probably represent a population that existed when the floor of this part of the Rift Valley was more extensively covered by fresh water than it is at the present time (Mohr, 1961) ; there is a close resemblance between these shells and those described by Bacci (1940) from a nearby locality. Thiele (1933) records living *B. unicolor* from near Lake Zwai, and it is possible that living populations remain to be discovered in some of the Rift Valley Lakes.

Rohrbach (1937) found specific anatomical differences between *B. unicolor* from the Nile at Cairo, and *B. capillatus* from N. Rhodesia. The male genital system of the Lake Tana specimens resembles that of the specimens from the Nile described by Rohrbach, but only a few of the Lake Tana females have a large number of embryos arranged in two or more rows as described by this author, who found up to 86 relatively small embryos in *B. unicolor* in contrast to 25–40 larger ones in *B. capillatus*. Though the number of embryos in the Lake Tana females is generally even less than that found in *B. capillatus* by Rohrbach, the arrangement in several rows when a large number is present, considered in conjunction with the anatomy of the male system, is evidence that this population is related to *B. unicolor* of the Nile. The small number of embryos present in the uterus may represent an adaptation to local conditions and it is probable that the anatomical and ecological distinctions between *B. unicolor* and *B. capillatus* will be found to be less clear than was thought by Rohrbach.

DISTRIBUTION. *Bellamya* is known in Ethiopia only from Lake Tana, near Lake Zwai, Lake Abyata (Bacci, 1943), and an unspecified locality in the southern part of the country (Martens). Many species which are probably conspecific with *B. unicolor* have been described in other parts of Africa ; the range of the genus extends down the basin of the River Nile to the Mediterranean and as far west as Senegal, the southern limit of distribution appears to be in Zululand.

Family **AMPULLARIIDAE**

PILA Röding

Pila speciosa (Philippi)

Ampullaria speciosa Philippi, 1849 : 18, and in Martin & Chemnitz, 1851 : pl. 11, fig. 2.

LOCALITY. Sidamo : 40 km. approx. W. of Dolo on Filtu road, near Ganale River, (1).*

Shell

The dimensions of the single empty shell are : L = 50 mm. ; ML = 38 mm. ; W = 45·5 mm.

REMARKS. This species is known from Somalia and the Kenya-Somalia border (Bacci, 1951 and Pain, 1961), and it is not surprising that its range extends for at least a short distance up the Ganale River into Ethiopia.

Family **VALVATIDAE**

VALVATA Müller

Valvata sp.

Valvata nilotica Jickeli, 1874 : 223, pl. 7, fig. 29 ; Bacci, 1940 ; *Valvata nilotica nilotica* ; Bacci, 1951 ; *Valvata nilotica* var. *scioana* ; Pollonera, 1888 : 62 ; *Valvata nilotica scioana* ; Bacci, 1940.

Valvata sp. Mandahl-Barth in Ayad, 1956.

LOCALITIES. Choa : 72 km. N. of Addis Ababa boundary of Debra Markos road, (17) ; 0·5 km. S. of Debra Berhan, (50) ; Lake Wonji, (10).

Shell (pl. 1, 4–9)

Two specimens are illustrated (pl. 1, 6 and 8) which represent the extremes of variation in the rate of descent of the whorl within a single sample (72 km. N. of Addis Ababa on Debra Markos road). In the Debra Berhan sample (pl. 1, 4 and 5) the range of the ratio L/W is 0·82–1·00 (10 shells). The umbilicus of shells from Lake Wonji (pl. 1, 7 and 9) is distinctly smaller than in the other samples. Fine transverse ribs are more or less regularly spaced on the apical whorls, where there is also a fine spiral sculpture.

Largest shell : L = 4·8 mm. ; ML = 3·0 mm. ; W = 6·0 mm. ; $3\frac{3}{4}$ whorls.

REMARKS. If *Valvata* of the Egyptian Nile are regarded as distinct from European species, it is possible that *V. saulcyi* Bourguignat 1853 should take precedence over *V. nilotica* Jickeli. As a detailed comparison between specimens of *Valvata* from Ethiopia, Egypt and Europe has not yet been made, a specific identification of the specimens in the present collection is impossible.

Variety *scioana* was described on the basis of three specimens from near Debra Berhan, in which the spire was considered to be less depressed, and the umbilicus more restricted, than in Jickeli's illustration of *V. nilotica.* Bacci (1940) observed that the majority of fossil specimens of *Valvata* from the vicinity of Lake Zwai were similar to var. *scioana,* and most of the shells in the present collection resemble this form in possessing a relatively rapidly descending whorl. The shells from Debra Berhan have even higher spires than the shells of *scioana* described by Pollonera : the mean ratio L/W is 0·90 (10 shells), compared to ratios of 0·66 (var. *scioana*) and 0·63 (*V. nilotica*) calculated from the dimensions given by Pollonera and Jickeli respectively. Restriction of the umbilicus does not appear to be necessarily associated with increase in the rate of descent of the whorl as suggested by Pollonera. Both low-spired and the high-spired shells from the north of Addis Ababa (pl. 1, 6 and 8) have a large umbilicus, but it is restricted in all the specimens from Lake Wonji.

Valvata revoili Bourguignat, 1889, is listed with reservation by Bacci (1951), and is considered to be a terrestrial species by Dr. G. Mandahl-Barth (pers. comm.).

DISTRIBUTION. *Valvata sp.* appears to have a wide range at moderately high altitudes in Ethiopia, occurring in both still and slow-flowing waters ; it is recorded by Ayad from south of Addis Ababa (Akaki) and from the Blue Nile near Lake Tana. This genus reaches the southern limit of its distribution in North Africa ; several species have been described from the lower course of the Nile and *V. tilhoi* Germain was described from the vicinity of Lake Chad.

Family **THIARIDAE**

MELANOIDES Olivier

Melanoides tuberculata (Müller)

Nerita tuberculata Müller, 1774 : 191 ; *Melania tuberculata ;* Blanford, 1870 ; Morelet, 1872 ; Jickeli, 1874 ; Bourguignat, 1872, & 1833, & 1885 ; Pollonera, 1898 ; De Rochebrune & Germain, 1904 ; Neuville & Anthony, 1908 ; Kobelt, 1910 ; *Melania* (*Melanoides*) *tuberculata ;* Thiele, 1933 ; Bacci, 1940 & 1941 ; *Melanoides* (*Thiara*) *tuberculata ;* Piersanti, 1940, & 1941 ; *Melanoides tuberculata ;* Ayad, 1956 ; Verdcourt, 1960 ; *Melania tuberculata* var. *costata* Bourguignat, 1864 : pl. 15, figs. 3 & 10 ; Pollonera, 1898.

Melania dembea Reeve, 1860 : pl. 23, fig. 161.

Melania curvicosta Pantanelli, 1897 : 204.

LOCALITIES. Arussi : 5 km. approx. S. of Adamitullo (between Lake Zwai and Bulbulla river), (6) *; Lake Zwai, N.W. shore, (1) ; River Awash, S. of Nazareth, (52). Eritrea : 20 km. approx. W. of Asmara on Massawa road. Sidamo : Lake Margherita, E. shore, (13).* Wallo : Lake Haik, (2).

Shell

Spiral ribs are present on the lowermost part of the shell, and tubercles are generally better developed than in the forms described by Mandahl-Barth (1954). In specimens from the River Awash, south of Nazareth, conspicuous transverse ribs are formed by the fusion of the large tubercles.

REMARKS. Specimens from near Saati (between Asmara and Massawa), with thick transverse ribs, were identified by Pollonera (1898) as var. *costata* Bourguignat. The specimens described above from the River Awash also resemble this form.

No specimens were found in Lake Tana, the type locality of *Melania dembea* Reeve, a form with moderately well developed transverse ribs that does not appear to differ significantly from *M. tuberculata*.

DISTRIBUTION. *M. tuberculata* is widely distributed in Ethiopia from near sea-level to an altitude of about 6,000 feet (Lake Tana) on the plateau. Its range includes most of Africa, excluding the Niger and Congo basins, and extends into the Arabian Peninsula and Asia.

Family **PHYSIDAE**

PHYSA Draparnaud

Physa sp.

LOCALITY. Choa : River Awash, below Koka Dam, (50).

Shell (pl. 2, 1)

The shell is moderately shiny ; many specimens have a light-coloured band a short distance from the outer lip. Fine transverse corrugations extend across the whorl, and are interspersed with short ones which are arranged in spiral rows on some parts of the surface.

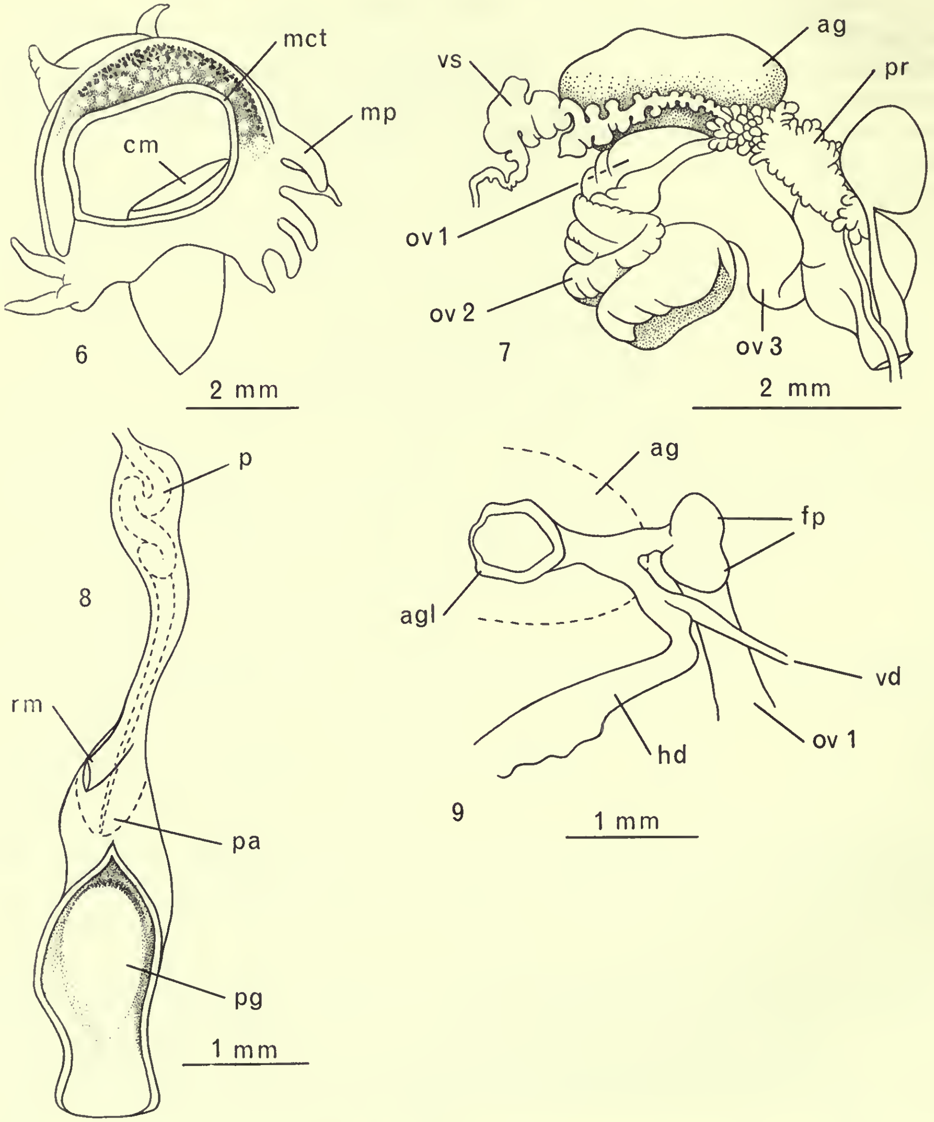
Anatomy (Text-figs. 6–9)

The distribution of pigment in the mantle (Text-fig. 6) forms light spots on a grey background, with small dark spots that are most numerous near the mantle edge. From beneath the anterior mantle edge projects a narrow flap that continues around the visceral hump with long finger-like projections from the posterior part.

The ovotestis consists of many acini scattered in the digestive gland. There are numerous blunt projections from the seminal vesicle region of the hermaphrodite duct (Text-fig. 7). Three regions may be distinguished in the female duct (Duncan, 1958) ; the proximal oviduct 1 is straight and narrow, and this leads to the junction between a highly convoluted oviduct 2 and the wide oviduct 3 which terminates in a short vagina. After leaving the junction with the hermaphrodite duct the vas deferens receives numerous prostatic diverticula, each of which is branched several times. A blunt papilla projects into the lumen of the preputium from the junction between the penis sheath and the preputium (Text-fig. 8) ; the tip of the penis usually reaches as far as the tip of the papilla, but the penis is considerably shorter in a few specimens. A preputial gland may be seen as a lightly pigmented oval area on the outer wall of the preputium, on the opposite side to the insertion of the retractor muscle. Internally the gland bulges into the lumen of the preputium, filling it almost completely. The junction between the male and female systems (Text-fig. 9) is similar to that described by Duncan (loc. cit.) for *Physa fontinalis*. The vas deferens (vd) arises from the hermaphrodite duct (hd) before this duct enters the albumen gland, but the junction between the hermaphrodite duct, oviduct 1, and the lumen of the albumen gland is surrounded by albumen gland tissue. Two fertilisation pockets project from the base of oviduct 1.

REMARKS. In both shell and anatomy the Ethiopian *Physa* resemble the southern European species *P. acuta* Draparnaud as described by Slugocka (1913) ; similar *Physa* have been examined (W.H.O.) from Kenya and Southern Rhodesia. These shells also closely resemble *P. borbonica* Férussac originally described from Mauritius. The elucidation of the relationships of the *Physa* in East Africa is a matter for future investigation.

DISTRIBUTION. *Physa* has not been reported previously from Ethiopia, but its occurrence might be expected as the genus is present in Egypt and Kenya. Cases of introduction of species of *Physa* in other parts of the world are known, and as *Physa sp.* was abundant in the single locality where it was found, it is likely that the snail has been recently established in Ethiopia and will become more widely distributed in the future.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FIGS. 6–9. *Physa* sp. from below Koka Dam. Fig. 6. Dorsal view of whole animal with visceral hump removed, pigmentation shown on anterior part of mantle only. Fig. 7. Distal genital organs. Fig. 8. Copulatory organ, penis and papilla shown by dotted lines and wall of preputium opened to show preputial gland. Fig. 9. Junction of male and female systems, position of albumen gland shown by dotted lines.

Family **LYMNAEIDAE**

LYMNAEA Lamarck

Lymnaea truncatula (Müller)

Buccinum truncatulum Müller, 1774 : 130 ; *Limnaea truncatula?* ; Jickeli, 1874 ; Bourguignat, 1883 ; Pollonera, 1898 ; Germain, 1904 ; Connolly, 1928 ; *Lymnaea truncatula* ; Wright & Brown, 1962 ; *Galba truncatula* ; Piersanti, 1941.

Limnaea peregra? ; Jickeli, 1874.

LOCALITIES. Arussi : 50 km. W. of Shashamanne on Soddu road, (4). Begemeder : 19–97 km. N. of Gondar on Asmara road, 6 samples, (100). Eritrea : 19 km. E. of Teramni on Decamere road, (1) ; 66 and 101 km. S. of Asmara on Addis Ababa road, (6) ; River Toquor near Mekerka, (1). Kaffa : 5 and 9 km. W. of Kombi, (2). Choa : 2–150 km. N. of Addis Ababa boundary on Debra Markos road, 5 samples, (15) ; Lake Wonji, (2) ; 29 km. W. of Addis Ababa on Lekemti road, (4). Wollo : Kombolchia village on Dessie road, (2) ; 8 km. N. of Dessie on Asmara road, (5). Harar : 71 km. on Carsa road from junction with Dire Dawa–Harar road, (20).

Shell (pl. 2,5)

There is a close resemblance to specimens from near Debra Markos described by Wright & Brown (1962).

Largest shell : L = 11·7 mm. ; ML = 6·2 mm ; W =6·0 mm. Several specimens in this sample are conspicuously malleated (pl. 2, 5).

Radula

In the 12 radulae examined the endocones of the first few lateral teeth are relatively smaller than in the lateral tooth illustrated by Wright & Brown (loc. cit.). In some lateral teeth the meso- and ectocones are elongated giving the teeth a bicuspid appearance which resembles the condition in *L. truncatula* from Aden (Wright, 1963b), though the cusps are shorter in the Ethiopian specimens.

REMARKS. The specimen of *L. peregra?* from the River Toquor near Mekerka illustrated by Jickeli (1874) closely resembles *L. truncatula* which was collected from the same locality during the recent expedition. However it is possible that living populations of European *Lymnaea* other than *L. truncatula* will be discovered in Ethiopia.

DISTRIBUTION. The majority of previous records of *L. truncatula* are from northern Ethiopia, but it has also been found in a sub-fossil condition as far south as the Nargi Plain, near Lake Stephanie (Piersanti, 1941). The present records suggest that this species is widely distributed at moderately high altitudes on both sides of the Rift Valley, and living populations may also occur at lower altitudes as is the case in Tanganyika (Mandahl-Barth, pers. comm.).

Lymnaea natalensis (Krauss)

Limnaeus natalensis Krauss, 1848 : 15, pl. 5, fig. 15 : Blanford, 1870 ; *Lymnaea natalensis* ; Mandahl-Barth in Ayad, 1956 ; Wright & Brown, 1962.

Limnaeus natalensis exsertus Martens, 1866 : 101, pl. 3, figs. 8 & 9 ; *Limnaea natalensis* var. *exserta* ; Jickeli, 1874 ; *Limnaea exserta* ; Bourguignat, 1883 ; Pollonera, 1898.

Limnaea orophila Morelet, 1868 : 87, pl. 7, fig. 4 ; *Limnaea natalensis* var. *orophila* Jickeli, 1874.
Limnaea caillaudi Bourguignat, 1883 : 89, pl. 10, figs. 100 & 101 ; Pollonera, 1898 ; Connolly, 1928 ; *Radix caillaudi ;* Bacci 1941.
Limnaea acroxa Bourguignat, 1883 : 90, pl. 10, fig. 94.
Limnaea alexandrina Bourguignat, 1883 : 92, pl. 10, figs. 95 & 96 ; De Rochebrune & Germain, 1904 ; *Limnaea exserta* var. *alexandrina ;* Pollonera, 1898.
Limnaea raffrayi Bourguignat, 1883 : 93, pl. 10, figs. 97 & 98 ; Pollonera, 1898.
Limnaea aethiopica Bourguignat, 1883 : 94, pl. 10, figs. 92 & 93 ; Neuville & Anthony, 1908.
Limnaea africana " Rüppell " Bourguignat, 1883 : 95, pl. 10, fig. 99 ; Neuville & Anthony, 1908.
Limnaea graveiri Bourguignat, 1885 : 23, fig. 6.
Limnaea soleilleti Bourguignat, 1885 : 24, fig. 7.
? *Radix pereger ;* Piersanti, 1940.

LOCALITIES. Arussi : Lake Zwai, (11). Begemeder : 308 km. S. of Asmara on Gondar road, (15) ; Lake Tana at Gorgora, (6). Choa : Tributaries of the River Awash at Akaki and Dukem, (12) ; River Awash below Koka Dam, (12); 22–318 km. N. of Addis Ababa on Asmara road, 4 samples, (75) ; 21 km. E. of Wolisso, (10). Eritrea : 22–83 km. S. of Asmara on Gondar road, 4 samples, (90) ; 15 km. approx. N.W. of Asmara on Cheren road, 2 samples, (30) ; River Toquor near Mekerka, (60) ; 3 km. E. of Teramni on Decamere road, (5) ; 66 and 101 km. S. of Asmara on Addis Ababa road, (30). Harar : 10 km. W. of Harar on Dire Dawa road, (30) ; Lake Aramyia, (50) ; 43 km. on Carsa road from junction with Dire Dawa–Harar road, (30). Kaffa : 26 km. W. of Sokuru, (6) ; 9 and 22 km. W. of Assendabo, (60) ; 13 and 14 km. W. of Jimma on Bonga road, (18) ; 34 and 38 km. N. of Jimma on Agarro road, (27) ; 4 km. E. of Jimma on Addis Ababa road, (24). Sidamo : Lake Margherita, (40) ; Neghelli, (40). Tigre : 0·5 km. W. of Adowa on Gondar road, (4) ; 222 km. S. of Asmara on Addis Ababa road, (5). Wollo : 26 km. S. and 0·5 km. N. of Kombolchia on Dessie road, (20) ; 1 km. W. of Batei, (23) ; 1 and 30 km. N. of Dessie on Asmara road, (80).

Shell (pl. 1, 10 and 11)

Five of the largest shells from all the samples were measured ; the extreme values of the mean ratio L/ML are 1·27 and 1·51, and the values for individual shells range between 1·23 and 1·54.

Largest shell (northern Choa) : L = 24·7 mm. ; ML = 18·7 mm. ; W = 14·5 mm.

Although there is a wide variation in the shape of the spire and the aperture through the whole series of samples, many of the samples have a distinctive appearance. A relatively high proportion of long-spired samples were obtained from Kaffa and Harar Provinces. Spiral rows of corrugations and depressions are present in many samples, but the extent to which this microsculpture covers each shell varies, and it may be confined to the apex only. Microsculpture is lacking from many of the shells collected in Harar, and in none of them is it well developed.

Anatomy

Both the intensity and arrangement of mantle pigmentation is very variable. A few unpigmented spots may be surrounded by a dense dark background, or at the other extreme pigmentation may be reduced to a fine network.

The genital system resembles that of specimens from Gojjam Province, Wright & Brown (1962). Some specimens from every sample were dissected, and in all of them the distal part of the prostate gland was swollen and a large internal fold was present.

Radula

The endocones and mesocones of the lateral teeth of several radulae (14 radulae from 3 samples examined) are more widely separated than in the teeth illustrated by Wright & Brown (loc. cit.).

REMARKS. Haas (1936) recognised 6 subspecies of *L. natalensis* in Africa, but Hubendick (1951) found no clear geographic pattern in the distribution of variation in shell and anatomical characteristics. However, Mandahl-Barth (1954) divided *L. natalensis* into 3 subspecies, of which *caillaudi* included certain E. African forms and all the species described from Ethiopia by Bourguignat. Specimens from the Victoria Nile, which are distinguished from *L. natalensis* by characteristics of the shell and prostate gland, are identified by the same author as *L. exserta* Martens, which was originally described from the highlands of Ethiopia. According to the proportions given by Mandahl-Barth the approximate values of the ratio L/ML vary between 1·13 (*L. natalensis nyansae*) and 1·50 (*L. exserta*). Many of the specimens in the present collection have the proportions of *L. natalensis caillaudi*, but as a considerable number conform to the subspecies *natalensis natalensis* and others to *L. exserta*, the material is not assigned to a subspecies.

None of the Ethiopian specimens dissected has a prostate gland like that described for *exserta* from the Victorian Nile by Mandahl-Barth, and the identity of the Uganda form with Martens' species must be considered doubtful. All the shells of *Lymnaea* obtained from Lake Tana, the type locality of *L. caillaudi*, closely resemble Bourguignat's description of this species and they are distinctive (pl. 2, 11) in comparison to all the other samples.

Radix pereger recorded by Piersanti (1940) appears to represent a small shell of *L. natalensis*.

DISTRIBUTION. As is the case in many other parts of Africa *L. natalensis* is widely distributed and abundant in Ethiopia, occurring in a variety of habitats including shallow fast-flowing streams and lakes.

Family **PLANORBIDAE**

Subfamily **BULININAE**

BULINUS Müller

Bulinus truncatus species group

Bulinus truncatus sericinus (Jickeli).

Bulinus truncatus (Audouin, 1827) sensu Connolly, 1928 : 177.

Physa contorta Michaud, 1829 sensu Martens, 1869 : 99 ; Blanford, 1870 : 476 ; Bourguignat, 1883 : 126 ; *Isidora contorta ;* Pollonera, 1898 : 12 ; Neuville & Anthony, 1906 : 274, fig. 9.

Isidora brocchii Ehrenberg, 1831 sensu Pollonera, 1898 : 12.

Physa natalensis? Kuster, 1841 sensu Martens, 1869 : 214 ; *Bulinus natalensis* ; Connolly, 1928 : 175, figs. 3 & 4 ; Bacci, 1940 : 455 ; Piersanti, 1941 : 276, fig. 40 ; *Physa natalica ;* Bourguignat, 1883 : 126.

Bulinus (*Diastropha*) *raymondianus* var. *porrecta* (Martens, 1874) sensu Piersanti, 1941 : 275, fig. 39.

Isidora sericina Jickeli, 1874 : 194, pl. 7, fig. 11 ; *Bulinus* (*Bulinus*) *sericinus ;* Mandahl-Barth, 1957b ; *Bulinus sericinus ;* Wright & Brown, 1962.

Isidora schackoi Jickeli, 1874 : 197, pl. 7, fig. 12 ; *Bulinus schackoi ;* Connolly, 1928 ; *Isidora schackoi* mut. *minima* Pollonera, 1898 : 12.

Physa coulboisi ? Bourguignat, 1888 sensu Neuville & Anthony, 1908 : 266, fig. 5.

Physopsis africana (non Krauss, 1848) Neuville & Anthony, 1908 : 266, fig. 5.

LOCALITIES. Arussi : Lake Zwai, (150) ; 50 km. approx. from Shashamanne on Soddu road, 2 samples, (100) ; River Awash, S. of Nazareth, 2 samples, (16). Begemeder : 38 km. N. of Gondar on Asmara road, (100) ; 66 km., 77 km., 97 km. and 116 km. N. of Gondar, (50) ; 279 km. N. of Gondar, (4) ; Lake Tana at Gorgora, (2). Choa : Lake Biete Mengest, (150) ; Lake Hora, (150) ; Lake Bishoftu, (20) ; swamp N. of Debra Zeit town, (100) ; Akaki River at Akaki, (40) ; Moggio River at Moggio, (5) ; River Awash on Addis Ababa–Jimma road, (2) ; 21 km. E. of Wolisso on Jimma road, (10) ; 10 km. W. of Ambo on Lekemti road, 2 samples, (20) ; Lake Wonji, (20) ; 16 km.–185 km. N. of Addis Ababa on Debra Markos road, 8 samples, (350) ; 67 km. and 130 km. N. of Addis Ababa on Asmara road, (40) ; 12 km. N. of Debra Sina, (2) ; 96 km. N. of Robi, (6). Eritrea : 22 km.–83 km. S. of Asmara on Gondar road, 4 samples, (90) ; 3 km.–38 km. N.W. of Asmara on Cheren road, 7 samples, (120) ; 66 km. S. of Asmara on Addis Ababa road, (20) ; River Toquor near Mekerka, (37). Harar : Lake Aramyia, (300) ; 17 km. (Langhei village) and 43 km. on Carsa road from junction with Dire Dawa–Harar road, (350). Kaffa : 26 km. approx. W. of Sokuru on Jimma road, (2) ; 22 km. W. of Assendabo on Jimma road, (25) ; 4 km. E. of Jimma on Addis Ababa road ; (20) ; 4 km. W. of Jimma on Bonga road, (40) ; 38 km. N. of Jimma on Agarro road, (2). Sidamo : Lake Margherita, east shore, (40). Tigre : 167 km. and 200 km. S. of Asmara on Addis Ababa road, (60) ; 341 km. S. of Asmara, (2) ; Lake Ashangi, N.E. shore, (100). Wollo : 1 km. W. of Batei, N. of Kombolchia road, (30) ; 1 km. within N. boundary of Dessie on Asmara road, (20) ; 8 km. and 30 km. N. of Dessie on Asmara road, (60) ; Lake Haik, S. shore, (130).

Shell (Text-fig. 10)

Because of the great variation in shell shape it is necessary to consider separately several more or less distinct forms. In many of the populations occurring on the

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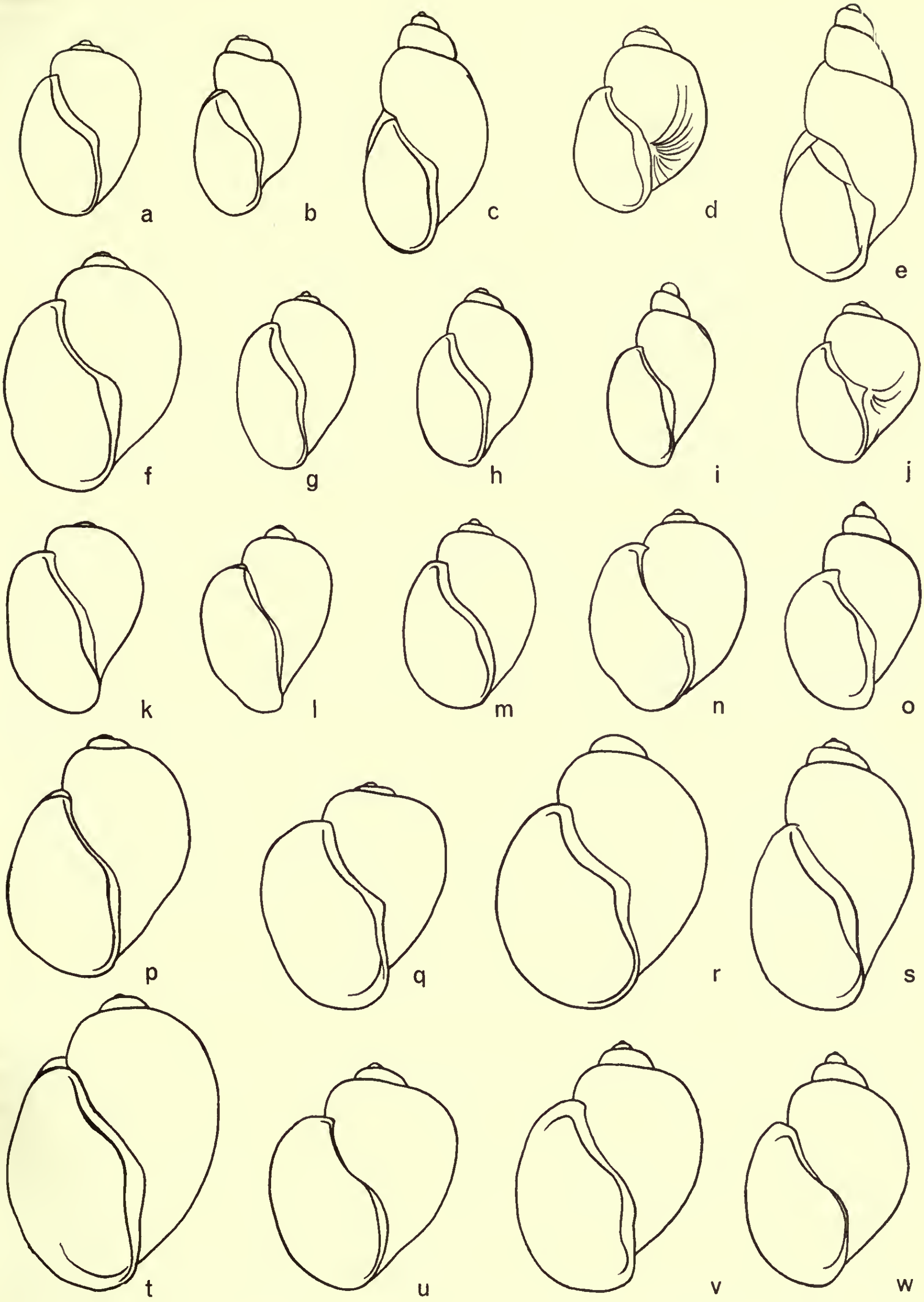
FIG. 10. *Bulinus truncatus sericinus* and *Bulinus* sp. (*truncatus* group), shell outlines drawn by camera lucida. a–t, *B. truncatus sericinus*. a–c, Choa, 72 km. N. of Addis Ababa on Debra Markos road. d, Eritrea, reservoir 4 km. N.W. of Asmara on Cheren road. e, Begemeder, 38 km. N. of Gondar on Asmara road. f, Choa, 12 km. N. of Debra Sina on Asmara road. g–i, Eritrea, River Toquor near Mekerka. j, Eritrea, 38 km. N.W. Asmara on Cheren road. k, m, Wallo, Lake Ashangi. l, Sidamo, Lake Margherita. n, o, Arussi, 5 km. S. of Adamitullo. p, t, Choa, Lake Hora. q, r, Choa, Lake Biete Mengest. s, Choa, swamp N.W. of Debra Zeit town. u–w, Arussi, *Bulinus* sp. from Lake Awasa.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plateau the shell is narrower than is usual in other parts of the range of *B. truncatus* in N.E. Africa, and in some populations the spire is unusually elongated (Text-fig. 10c and e). Further characteristics, developed to a variable extent, are the relatively great length of the ultimate whorl, and the somewhat shouldered appearance of the apical whorls. Some samples contain a wide range of shell shapes (Text-fig. 10 a–c, g–i), but others are uniform. The kind of shell described above is common at moderately high altitudes in Ethiopia, but in the same regions populations with small, widely umbilicate, short-spired shells occur (d and j), and also a few populations reaching a relatively large maximum size (f). Maximum individual size varies widely between populations, generally the largest shells do not exceed 15 mm., and many populations appear to be full grown at less than 10 mm. Exceptionally large specimens were present in a reservoir near Asmara.

Largest shell : L = 21·5 mm. ; ML = 12·9 mm. ; W = 11.8 mm. ; 5 whorls. Transverse ribs, arranged regularly on the upper whorls, are present in at least some shells in every sample, and are overlain by flaps of periostracum in many specimens. A faint spiral sculpture is occasionally present. The columella is slightly twisted in some samples. Four samples of particular interest from the plateau region are described below.

1. Eritrea : River Toquor near Mekerka (Text-fig. 10, h–j). Type locality of *Isidora schackoi* and *I. sericina* Jickeli, 1874. Text-figure 10 illustrates the variation in the length of the spire.

Largest shell : L = 10·7 mm. ; ML = 7·3 mm. ; W = 6·6 mm. ; 4 whorls.
Ratio L/ML ranges between 1·15 and 1·50 (37 shells).

2. Begemeder : 38 km. N. of Gondar (pl. 2, 2 and Text-fig. 10e). Exceptionally long-spired shells, some of which have the surface of the ultimate whorl conspicuously malleated.

Largest shell : L = 13·3 mm. ; ML = 8·0 mm. ; W = 6·8 mm. ; 4½ whorls.
Ratio L/ML ranges between 1·51 and 1·80 (20 shells).

3. Tigre : Lake Ashangi (Text-fig. 10m). Relatively short-spired shells with rounded apertures. Fine, irregular transverse ribs are present, and faint spiral sculpture is present on the apex.

4. Wollo : Lake Haik. An exceptionally small form.

Largest shell : L = 8·4 mm. ; ML = 6·5 mm ; W = 5·5 mm. ; 3¼–3½ whorls, (sample of approx. 100).

Populations that are similar to some of those of the plateau were found at lower altitudes south of Addis Ababa : between Addis Ababa and Debra Zeit ; between Shashamanne and Soddu, and in the River Awash south of Nazareth. These localities, with the exception of the River Awash, are elevated in relation to the floor of the Rift Valley. The populations occurring in the Bishoftu Crater Lakes at Debra Zeit, and in the Rift Valley Lakes, are distinctive and are described below.

5. Choa : Bishoftu Crater Lakes (Text-fig. 10, p–r and t). Collections were made in Lakes Biete Mengest, Hora, and Bishoftu (see Mohr, 1961 for terminology). All the shells are relatively wide, with a more or less evenly rounded aperture that has an obtuse angle above.

Largest shell : L = 14·2 mm. ; ML = 9·8 mm. ; W = 10·5 mm. ; 4+ whorls, (L. Biete Mengest).

Ribs are well developed in both the shell and the periostracum, and spiral sculpture is exceptionally well developed in the Lake Hora population. In a nearby swamp (W. of Debra Zeit town), the shells have longer spires and narrower apertures (Text-fig. 10s).

6. Lakes Zwai and Margherita (Text-fig. 10k and l). The shells have relatively large apertures compared to those of the plateau populations.

Anatomy

The mantle and genital organs of *B. truncatus sericinus* from near Debra Markos were described by Wright & Brown (1962). Mantle pigmentation, like shell shape, is often characteristic of a particular population, but the value of pigmentation as a taxonomic character is reduced by the great variation that may be observed in samples from a small area. No characteristics in the gross morphology of the genital organs have been observed that can be correlated with the various shell shapes in the present collection, but it is likely that the size at which sexual maturity is reached in each population is related to the maximum size achieved in that habitat.

Wholly aphallic specimens (which were not present in the samples from near Debra Markos) are present in several of the samples, but the aphallic condition does not appear to be correlated with either shell shape or geographical distribution. Of 20 samples examined, 7 contain aphallic individuals. The proportions of aphallic specimens found range between 8 per cent. (Lake Bishoftu, 25 specimens), 92 per cent. (Lake Zwai, 25 specimens), and 100 per cent. (Lake Margherita, 10 specimens).

Radula (Text-figs. 19–21)

More or less distinctive characteristics are present in each sample of radulae that has been examined, and it is likely that a detailed analysis would reveal a variation comparable to that observed in the shell. The central tooth usually bears two cusps, but in one radula the entire row of centrals bears a single median cusp. The mesocone of the lateral teeth is occasionally bluntly pointed, but generally approaches an arrow-head shape which is very obvious in the Lake Ashangi specimens (Text-fig. 21). One or two interstitial cusps (Wright & Brown, loc. cit.) may be present on the lateral teeth. Transition between the lateral and marginal teeth usually takes place between teeth 6 and 8 with the development of additional cusps between the endo- and the mesocone, and lateral to the ectocone (Text-figs. 19, 20). The mesocone can be recognised in many of the marginal teeth, but up to nine more or less similar cusps may be present on the median side of these teeth, and a variable number of small cusps is present on the lateral side.

Folds or ridges, which appear to correspond to the " fluting " described by Stiglingh et al (1962), are present on the endo- and mesocones of the lateral teeth of many specimens. Folding is particularly well developed on the cusps of the lateral teeth of specimens from 38 km. N. of Gondar, which have broadly based endocones of a characteristic shape (Text-fig. 19).

REMARKS. Apart from locally described species and varieties, and a single shell identified by Neuville & Anthony as *B. coulboisi*, shells of *Bulinus* (*Bulinus*) from

Ethiopia have been identified as either Egyptian or South African species by previous authors. Mandahl-Barth (1960) and Wright & Brown (1962) regard the locally described forms as synonymous with *B. sericinus* (Jickeli), belonging within the *B. truncatus* group. The present collection provides information about the variation of the *Bulinus truncatus* group which is of value in the interpretation of the interrelationships between the Ethiopian forms and their relationship to the *Bulinus* of other parts of Africa.

Only 37 moderately sized specimens were collected in the type locality of *B. sericinus* and *B. schackoi*, but the series contains sufficient variation in spire height to encourage the view that elongated shells of the *schackoi* type may be considered as part of the continuous variation of a population of *B. sericinus* (Wright & Brown, loc. cit.). However, although some other samples in the present collection contain a more or less complete intergradation between the *sericinus* and *schackoi* types of shell, many large samples contain a comparatively restricted range of variation. Sample 2 described above consists almost entirely of long-spired *schackoi* shells, of which the range of variation of L/ML scarcely overlaps that of any other populations. Such distinctive populations may be produced either by genetic characteristics of the snails, or ecophenotypic effects of the habitat, or both factors acting together. The occurrence of small *schackoi* snails together with small *sericinus* in the same habitat, where they have presumably experienced the same environmental influences, is evidence that there is some genetic difference between the forms.

It has long been appreciated that there is a close resemblance between the shells of some Ethiopian *Bulinus*, and those of *B. natalensis* (Krauss) of South Africa. Specimens from northern Ethiopia have been identified as *natalensis* (Martens, 1869 and Bourguignat, 1883), as have examples from in or near the Rift Valley Lakes (Connolly, 1928, Bacci 1940, Piersanti, 1941). Connolly divides specimens from the Bishoftu Crater Lakes (Bishoftu and Hora Harsadi) and Lake Zwai into two forms, one of them probably conspecific with *natalensis* and the other somewhat different, which occurred together in one lake (Bishoftu). Specimens similar to those described by Connolly were collected during the recent expedition in Lakes Zwai, Bishoftu, and Biete Mengest (=Hora Harsadi of Connolly). In addition, a further population has been found (Lake Hora, see 5 above) with exceptionally well developed spiral sculpture. All the lateral radula teeth examined in Ethiopian specimens have arrow-head shaped cusps, in contrast to the South African *Bulinus* (*Bulinus*) which are placed in the *Bulinus tropicus* group (including *natalensis* Krauss), having sharply pointed cusps (Mandahl-Barth, 1957b, and 1962). However, a close relationship between Ethiopian and South African forms is not precluded, as a form of *B. tropicus* from Transvaal which possesses arrow-head shaped cusps has been described by Stiglingh et al. (1962) which is considered by Mandahl-Barth (pers. comm.) to represent *B. natalensis* (Krauss) and to belong within the *truncatus* group.

It is thus a matter for conjecture whether certain populations of *Bulinus* (*Bulinus*) occurring in Ethiopian lakes are related most closely to South African *Bulinus* with arrow-head shaped cusps, to populations of the *B. truncatus* group occurring at relatively low levels in N.E. Africa, or to *B. truncatus sericinus* of the Ethiopian plateau. Dr. J. B. Burch (in. litt.) has found differences in chromosome number between several populations of the *B. truncatus* group in N.E. Africa (see under *Bulinus* sp. below), and it is to be hoped that such studies will be of value in elucidating the relationships discussed above. At present, the inclusion of the varied forms in *B. truncatus sericinus* is provisional.

Distribution. *B. truncatus sericinus* is widely distributed in Ethiopia above an altitude of about 1,500 m. (5,000 ft.), and has been found at 2,945 m. (9,600 ft.) (38 km. N. of Gondar). This subspecies is regarded as including *Bulinus* from Western Aden Protectorate (Wright, 1963b), but the records of *B. sericinus* from other parts of Africa probably refer to other forms of *Bulinus*.

Bulinus sp.

Localities. Arussi : 5 km. approx. S. of Adamitullo (between Lake Zwai and Bulbulla River) (6)*. Sidamo : Lake Awasa (400).

Shell (pl. 2, 4 and Text-figs. 10u–w)

Most of the shell length is contributed by the ultimate whorl, the apical whorls forming a small sharp spire. The aperture is large, more or less evenly rounded, and has an obtuse upper angle that is frequently more than 90 degrees. As a result of the steep curvature of the upper part of the whorls the suture is deep. Fine transverse ribs are present, but there are no free flaps of periostracum. Spiral sculpture is well developed on the apices of many shells, and is occasionally present on some parts of the ultimate whorl. Fresh shells are pale straw-coloured or almost white.

Largest shell : L=13·8 mm.; ML=10·5 mm.; W=10·4 mm.; four and three-eighths whorls.

Anatomy

Out of 25 specimens dissected, 9 are aphallic and 6 lack penis sheaths.

Radula (Text-fig. 22)

The lateral teeth have arrow-head shaped cusps but the radula teeth appear to be significantly smaller than in specimens of the same size from plateau populations of *B. truncatus sericinus*.

Remarks. Living snails have a characteristic blue-grey bloom ; approximately 10 per cent. of those collected lacked dark pigment and appeared to be albinos.

Dr. J. B. Burch (1964) finds that the haploid chromosome number of specimens collected in Lake Awasa is 18, in contrast to 36 in *B. truncatus* from Egypt and Iran, and 72 in laboratory bred stock of *B. truncatus sericinus* collected by Dr. C. A. Wright in Western Aden Protectorate. Burch (1960) has also reported a haploid number of 18 in the *Bulinus tropicus* group. The low chromosome number of the Lake Awasa *Bulinus*, and the similarity of the shells to sub-fossil shells from the vicinity of Lake Zwai (Text-fig. 10), are facts that in conjunction suggest that the form may be an ancient one now restricted in range.

Bulinus africanus species group

B. africanus ovoideus (Bourguignat)

*Physopsis ovoide a*Bourguignat, 1879 : 16 ; *B.* (*P.*) *africanus ovoideus* ; Mandahl-Barth, 1957 : pls. 17 & 18.

LOCALITIES. Begemeder : 14 km. N. of Medhanie Alem on Asmara road (27) ; Lake Tana at Gorgora (21) ; 8 km. N. of Gorgora (5). Kaffa : 44 km. E. of Jimma town boundary on Addis Ababa road (80).

Shell

The outstanding characteristics of each sample are described below.

1. Medhanie Alem (pl. 2, 9, 12). The spire is relatively short and sharp and the surface of the ultimate whorl is evenly curved with no trace of a shoulder. Spiral microsculpture is very well developed on the apex, and extends nearly to the aperture in several specimens. Where the microsculpture extends to the lowest whorl, the nodules become elongated and scarcely elevated from the surface, giving the appearance of rows of striae.

Largest shell : L=17·7 mm.; W=13·1 mm.; ML=11·4 mm.; 4¾–5 whorls.

2. Lake Tana (pl. 2, 8, 11). The spire is relatively longer than in the preceding sample but the apical whorls are less exserted and not sharply pointed. The whorls are flattened near the suture so that a blunt shoulder is formed. Spiral microsculpture similar to that described above is present, but is less distinct. All the larger shells have a thickened ridge at approximately the same distance from the aperture, indicating that growth has been temporarily interrupted.

Largest shell : L=11·7 mm.; ML=9·1 mm.; W=7·8 mm.; 4¾ whorls.

3. Kaffa (pl. 2, 13–15). The larger specimens are narrow with rounded apical whorls and comparatively long spires. The shell colour is not brown as in the preceding samples but whitish to pale horn. The aperture lengths and shell widths are smaller than in Medhanie Alem shells of the same length over the whole of the size range, and more whorls have been completed at the same length. Microsculpture similar to that of the preceding samples is present. At, or near, the aperture of all but the smallest shells is a light coloured band which marks a temporary cessation of growth.

Largest shell : L = 16·2 mm. ; ML = 11·4 mm. ; W = 9·3 mm. ; 5 whorls.

Anatomy

In all the samples the mantle is similarly pigmented with distinct dark blotches (Text-fig. 18). The penis sheath is longer and broader than the preputium, the range of PS/PP lying between 1·07 and 1·73 (20 specimens dissected).

Radula (Text-fig. 24)

Transition between the lateral and the marginal teeth is marked by the development of a small cusp between the endocone and the mesocone, which usually takes place at the 10th tooth (12 radulae examined).

REMARKS. The shells collected on the north shore of Lake Tana show some resemblance to *Bulinus globosus*. Similar shells collected by Dr. N. Ayad near Bahr Dahr on the south shore were identified as this species by Mandahl-Barth (in

Ayad, 1956). However, the copulatory organs of the specimens from Gorgora are similar to those from near Medhanie Alem, the shells of which resemble *B. africanus ovoideus*, and it is probable that this species is present on both the north and south shores of the lake. With regard to the large number of apparently suitable habitats that were searched in which no *B. africanus* were found, it may be concluded that populations are widely separated. This kind of distribution would favour the development of distinct local characteristics as described above in the case of the shell.

DISTRIBUTION. The present records from Begemeder appear to be the most northerly for *B. africanus* in East Africa. *B. africanus ovoideus* appears to have a wide range on the Ethiopian plateau but is not abundant ; it is widely distributed in Kenya and Uganda and extends into the Congo and Tanganyika (Mandahl-Barth, 1957b).

Bulinus ugandae Mandahl-Barth

Bulinus (*Physopsis*) *globosus ugandae* Mandahl-Barth, 1954 : 114, figs. 55a–h ; *B.* (*P.*) *ugandae* Mandahl-Barth, 1957.

LOCALITY. Sidamo : Lake Margherita, east shore (16).

Shell (pl. 2, 6, 7 and 10)

The majority are moderately high-spired, with rounded whorls that are more or less shouldered near the suture.

Largest shell : L = 14·7 mm. ; ML = 10·9 mm. ; W = 11·3 mm. ; 4½ whorls. The upper angle of the aperture is obtuse and frequently a right-angle ; the inner edge of the aperture is folded narrowly over the umbilicus which is open. Truncation of the columella is so slight in many specimens that it resembles the oblique twisting occasionally present in *Bulinus* (*Bulinus*). Irregular transverse ridges of varying size are scattered over the whole shell surface, and the second whorl of some specimens bears spiral ridges which cross the transverse ridges forming a poorly defined network of elevations and pits. In some specimens there is a very fine spiral microsculpture over the rest of the shell surface formed by rows of shallow ridges and furrows but never consisting of well defined nodules as in *B. africanus ovoideus*.

Anatomy (Text-fig. 17)

In contrast to *B.* (*P.*) *africanus ovoideus* the mantle lacks definite patches of pigment and is evenly grey in appearance (Text fig. 17). On the inner surface there is a long fold between the rectum and the kidney extending as far back as the posterior end of the kidney, and a large fold along the whole length of the surface of the kidney.

As all the copulatory organs are everted the length of the penis sheath can only be estimated as equal to or slightly longer than the preputium.

Radula (Text-fig. 23)

Transition between the lateral and the marginal teeth takes place earlier than in the preceding species, at about the 8th or 9th tooth (4 radulae examined).

REMARKS. Although columellar truncation and spiral microsculpture are almost absent in several shells, the presence of a long renal fold confirms that these specimens belong to the *Bulinus africanus* species group. There is a close resemblance to shells of *B. ugandae* from Kosti (Sudan) and Kisumu (Kenya) figured by Mandahl-Barth (1957b, figs. 40d and 41b), and it is not surprising that the range of this species should extend into south-west Ethiopia. Comparison with *B. abyssinicus* (Martens) from Somalia (Mandahl-Barth, 1957c) shows that in general appearance the Lake Margherita specimens are closer to *B. ugandae*. However, as the original description states that spiral microsculpture is completely absent from the apex of *B. ugandae*, the presence of some spiral microsculpture in the Lake Margherita shells might be taken to indicate a close relationship with *B. abyssinicus*. This is not an important point of resemblance though, because as *ugandae* was originally described as a subspecies of *B. globosus* they are probably closely related, and the presence of slight spiral sculpture in *ugandae* is not surprising as it is frequently well developed in *globosus*.

DISTRIBUTION. It is likely that *B. ugandae* occurs elsewhere in Ethiopia but the species is probably rare as only a single colony was found during several days collecting on the shore of Lake Margherita. Five specimens with eroded apices collected in Lake Stephanie and identified by Piersanti (1941) as *B.* (*P.*) *africanus* may represent *B. ugandae*. The range of this species is confined to north-east Africa including Uganda, Tanganyika, Kenya and Sudan.

Bulinus forskali species group

Bulinus forskali (Ehrenberg)

Isidora forskalii Ehrenberg, 1831 : 20 ; Jickeli, 1874 ; Pollonera, 1898 ; Neuville & Anthony, 1908 ; *Physa forskalii ;* Martens, 1869 ; Morelet, 1872 ; Bourguignat, 1883 ; Neuville & Anthony, 1906 ; *Pyrgophysa forskalii ;* Neuville & Anthony, 1905 ; *Bulinus forskali ;* Connolly, 1928 ; Haas, 1932 ; *Bulinus* (*Pyrgophysa*) *forskalii ;* Bacci, 1941 ; *Bulinus* (*Bulinus*) *forskalii ;* Mandahl-Barth, 1957b & 1960.

Physa forskalii var. *elatior* Martens, 1866 : 100.

Bulinus (*Isidora*) *forskali* var. *cylindrica* Piersanti, 1941 : 275, fig. 38.

Pyrgophysa scalaris (non Dunker, 1845) Neuville & Anthony, 1905.

LOCALITIES. Arussi : Lake Zwai, N.W. shore (15) ; 1 km. S. of River Awash on Nazareth-Asella road (15). Begemeder : Lake Tana at Gorgora (5). Sidamo : Lake Margherita, east shore (50) ; army barracks at Neghelli (2) ; artificial pool 10 km. approx. S. of Uachile Wells (50). Wollo : 62 km. S. of Kombolchia on Addis Ababa road (20).

Shell (pl. 3, 1 and 2)

Few of the shells in any sample exceed 8·5 mm. in length, at which size about 5½ whorls have been completed (Text-fig. 27).

Largest shell : L = 10·6 mm. ; ML = 4·3 mm. ; W = 3·5 mm. ; 6¼ whorls (Lake Tana). The aperture occupies less than half of the total length of the shell length in specimens of more than 3 mm. shell length (Text-figs. 25 and 26). The shoulder on the upper whorls is acute in many specimens, and frequently bears a distinct carination (pl. 3, 2). Irregular growth ridges of varying size are present, and there are regularly spaced ribs on at least the second and third whorls of most shells.

Anatomy (Text-figs. 11 and 28)

The copulatory organ (Text-figs. 11a–c and 28) is small in comparison to that of *B. scalaris*, with a penis sheath that is narrower than the preputium and less than twice its length in most specimens. In the Lake Margherita sample the ratio PS/PP ranges between 0·95 and 2·42 with a mean of 1·57 (14 specimens).

Remarks. *Bulinus fischerianus* (Bourguignat), the only species of the *Bulinus forskali* group originally described from Ethiopia, is provisionally placed within the synonymy of the *B. scalaris* (Dunker) in the present paper (see below). As the only other members of the *forskali* group described in north-east Africa are *B. forskali* (Ehrenberg) and two other Egyptian forms belonging within the synonymy of this species (Mandahl-Barth, 1957b), it remains to compare the present *Bulinus* with *B. beccarii* (Paladilhe, 1872) which has recently been recorded by Wright (1963b) from the Western Aden Protectorate.

Shells of the Ethiopian specimens here identified as *B. forskali* have the transverse ribs and carination far more strongly developed than do specimens of *B. beccarii* from Western Aden Protectorate. Wright described differences in the shell and radula between *beccarii* and the other members of the *B. forskali* group, and concluded that the part played by *beccarii* as an intermediate host of *Schistosoma haematobium* suggested a relationship with *B. senegalensis* or *B. cernicus*. There is no evidence that the Ethiopian *Bulinus* in question act as an intermediate host of *S. haematobium*, and the waters in which they were found are still in contrast to the slowly flowing water inhabited by *beccarii*. As no significant differences have been observed between shells of Ethiopian *forskali* and specimens from Egypt and Kenya, it is concluded that the Ethiopian populations form part of the extensive north-east African range of this species.

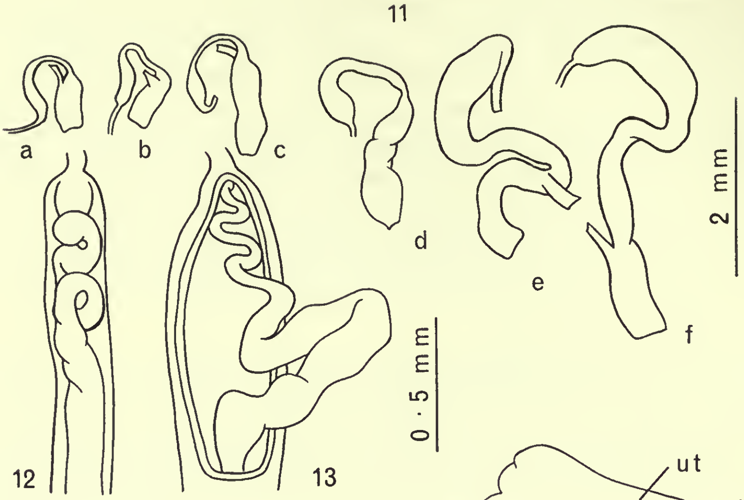
Distribution. *B. forskali* is recorded from relatively low altitudes in southern Ethiopia by Martens (1866), Haas (1932) and Piersanti (1941), and there are several records in eastern Eritrea also from low altitudes. The species is recorded from Lake Zwai (Connolly, 1928), and from southern Choa (Neuville & Anthony, 1908). The present records go some way towards connecting these scattered areas of distribution, and suggest that the species has a widespread distribution in the south extending at least as far north as the River Awash at an altitude of about 5,000 feet. *B. forskali* appears to be absent from the vicinity of Addis Ababa and Asmara, but its presence in southern Wollo Province and Lake Tana suggests that there is also an extensive range of scattered distribution on the plateau. *B. forskali* is widely distributed in Egypt and Africa south of the Sahara, but does not appear to have been recorded at such high altitudes outside Ethiopia.

Bulinus scalaris (Dunker)

Physa scalaris Dunker, 1845 : 164, 1853 : pl. 2, figs. 5 & 6.

Physa fischeriana Bourguignat, 1856 : 146, pl. 2, figs. 1–3 ; Bourguignat, 1883 ; *Physa fischeri ;* De Rochebrune & Germain, 1904.

Localities. Begemeder : 4 km. N. of Gorgora to 248 km. S. of Asmara, 10 samples (230). Kaffa : 44 km. E. of Jimma town boundary (17).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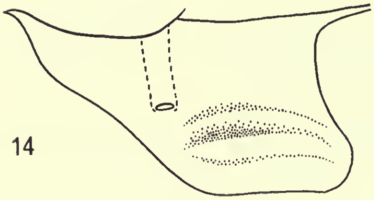

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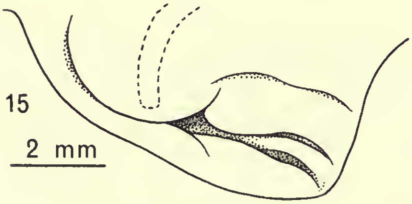

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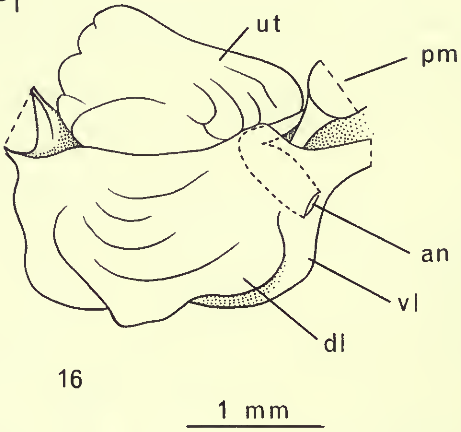
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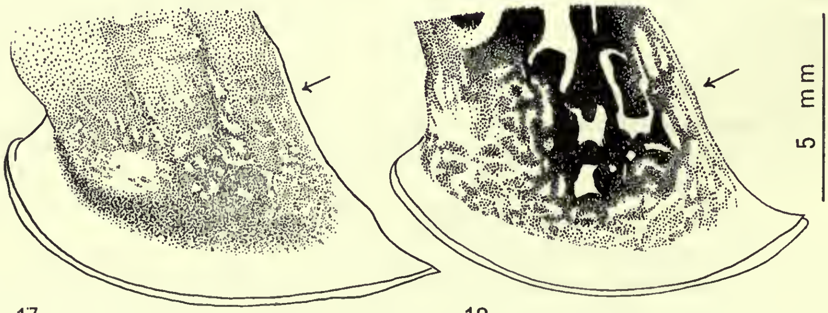


17

18

Shell (pl. 3, 3)

Maximum individual size is greater than that of *B. forskali* in most of the samples. Largest shell : L = 12·5 mm. ; 6 whorls. The spire is relatively less narrow than that of *B. forskali*, the rate of increase in the number of whorls is slightly slower (Text-fig. 27), and the length of the aperture tends to be longer (Text-figs. 25 and 26). There is no shoulder on the lower whorls, but the upper whorls of many specimens are shouldered, though usually less acutely than in *B. forskali*. In a few specimens a slight carination is present. Regularly spaced ribs which are less well defined than in *B. forskali* are present on the upper whorls, and fine spiral sculpture is present in several samples.

Anatomy (Text-figs. 11, 13 and 28)

The copulatory organ (Text-figs. 11e and f) is larger than that of *B. forskali*, with a penis sheath that is wider than the preputium and at least twice its length in the majority of specimens. In a sample from 4 km. N. of Gorgora the ratio PS/PP ranges between 1·68 and 5·00 with a mean of 3·01 (19 specimens). The epiphallus (Text-fig. 13) is not as long as that depicted by Mandahl-Barth (1957b, p. 87), but from the length of the everted penis it is evident that the epiphallus is capable of extending at least twice the length of the sheath.

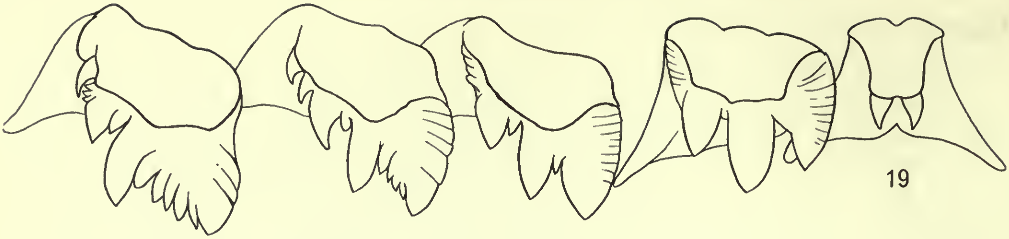
The vagina is everted to some extent in all of the specimens examined ; this condition was first recorded in *B. scalaris* by Mandahl-Barth (1960) and appears to be characteristic of fixed specimens of this species.

REMARKS. Wright (1963a) points out that shells of *B. scalaris* (including specimens in the type series) are occasionally somewhat shouldered, and this is also the case in the present collection. It is thus impossible to contrast *B. scalaris* with *B. forskali* as having " not the faintest trace of a shoulder angle " (Mandahl-Barth, 1957b). However, *B. scalaris* can readily be distinguished from *B. forskali* by the shape and size of the copulatory organ, and the shape of the shell.

Bulinus fischerianus (Bourguignat) is tentatively included in the synonymy above because of the close resemblance between Bouguignat's figure of this species and many of the shells of *B. scalaris* in the present collection.

DISTRIBUTION. The shell recorded from the River Moggio by Neuville & Anthony (1905) as *scalaris* and later (1908) figured as *forskali*, closely resembles the former species, which may thus occur at relatively low altitudes in southern Choa.

FIG. 11. Copulatory organs of a *B. forskali* from Lake Margherita,; b. *B. forskali* from Lake Zwai ; c. *B. forskali* from 62 km. S. of Kombolchia ; d. *Bulinus* sp. (*forskali* group) ; e. *B. scalaris* from 47 km. N. of Medhanie Alem ; f. *B. scalaris* from 4 km. N. of Gorgora. All specimens between 8·3 and 9·8 mm. shell length. FIG. 12. *Bulinus* sp. (*forskali* group), epiphallus seen by transparency through wall of sheath. FIG. 13. *B. scalaris* from 4 km. N. of Gorgora, wall of sheath dissected away to expose epiphallus. FIG. 14. *Ancylus* sp. from 15 km. N. of Dilla, pseudobranch. FIG. 15. *Ancylus fluviatilis* from 45 km. N. of Gondar, pseudobranch. FIG. 16. *Burnupia caffra* from 59 km. N. of Addis Ababa on Debra Markos road, dorso-lateral view of pseudobranch. FIG. 17. *Bulinus ugandae* from Lake Margherita, outer surface of mantle. FIG. 18. *Bulinus africanus ovoideus*, outer surface of mantle.



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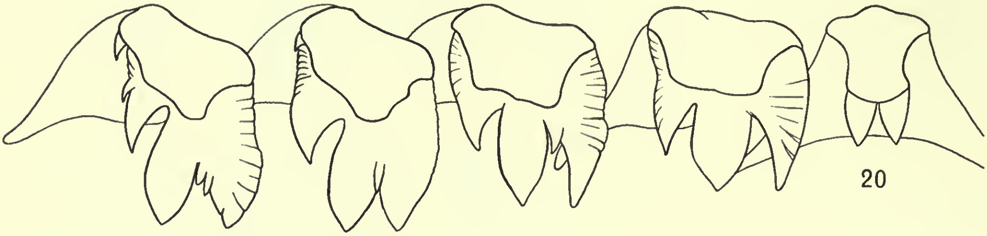

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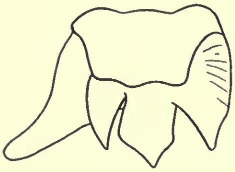

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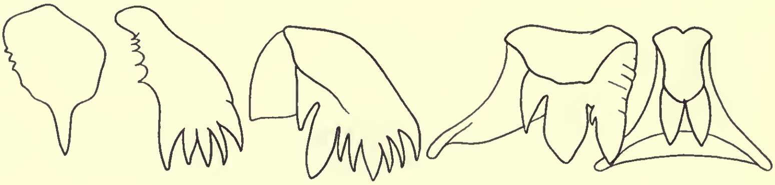

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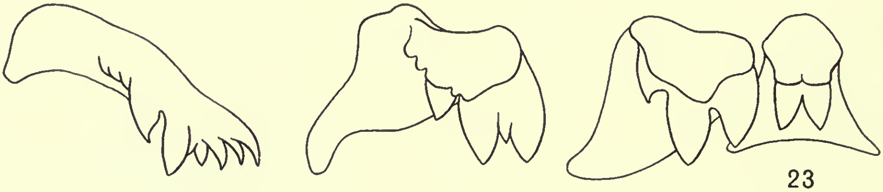

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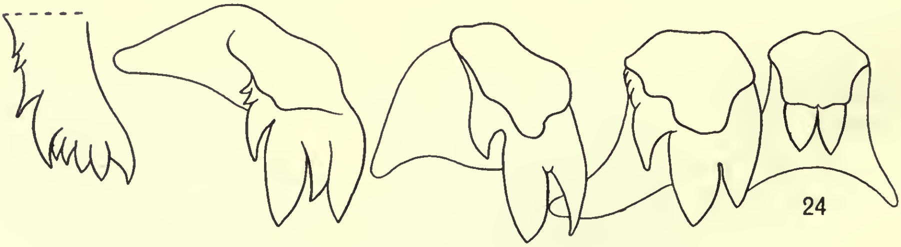


24

0 · 025 mm

FIGS. 19–24. Radula teeth. FIGS. 19–21. *Bulinus truncatus sericinus*. FIG. 19. 38 km. N. of Gondar, central, 1, 6, 7, and 8. FIG. 20. River Toquor near Mekerka, central, 1, 6, 7, and 8. FIG. 21. Lake Ashangi, 1.

FIG. 22. *Bulinus* sp. (*truncatus* group) from Lake Awasa, central, 1, 10, 23 and 24. FIG. 23. *Bulinus ugandae* from Lake Margherita, central, 1, 9 and 15. FIG. 24. *B. africanus ovoideus* from 5 km. W. of Assendabo. central, 1, 9, 12 and 26.

However, other shells figured by these authors from Goro Gomoto, a nearby locality, resemble *forskali* more closely, and as populations of *forskali* are known from the south and east of this area (see records for Arussi), the Neuville & Anthony records are provisionally regarded as representing *B. forskali.*

Two widely separated groups of populations of *B. scalaris* have been found which may be part of a scattered distribution in small temporary habitats throughout the plateau of Ethiopia. The record of *B. fischeri* by De Rochebrune & Germain (1904) from the S.E. side of the Rift Valley may also represent this species.

Elsewhere in Africa *B. scalaris* is known to have a scattered distribution in Angola, Congo, N. Rhodesia, Kenya and Uganda.

Bulinus sp.

LOCALITY. Begemeder : 4 km. N. of Medhanie Alem (approx. 322 km. S. of Asmara on Gondar road) (100).

Shell (pl. 3, 4)

Similar to that of *B. scalaris* apart from the relatively deeper suture.

Largest shell : L = 12·5 mm. ; ML = 5·4 mm. ; W = 4·9 mm. ; $6\frac{1}{4}$ who ls.

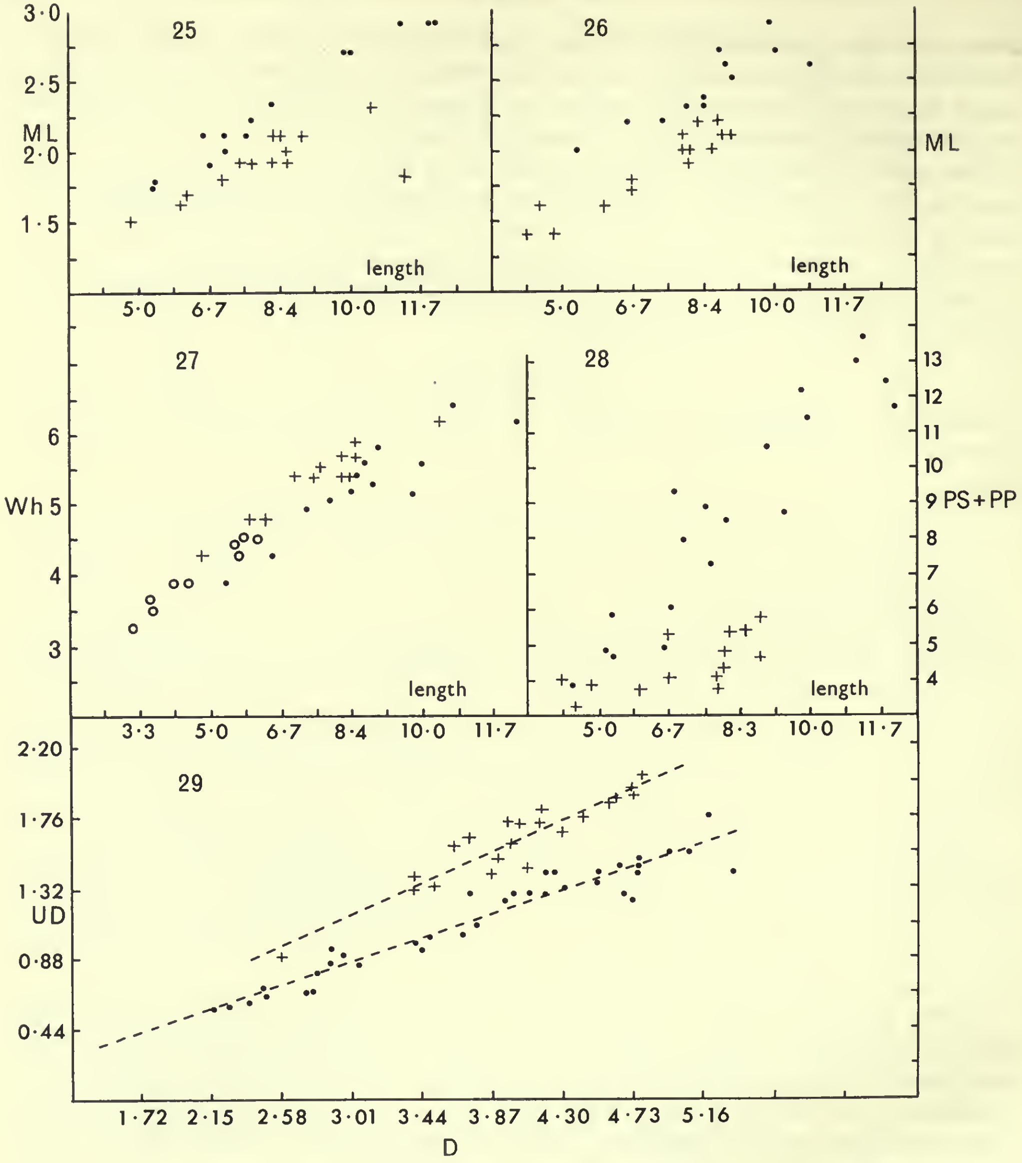
Anatomy (Text-figs. 11 and 12)

The copulatory organ (Text-fig. 11) is intermediate in size between that of *B. forskali* and *B. scalaris* but resembles that of *forskali* in the relationship between the dimensions of the penis sheath and the preputium. The ratio PS/PP varies between 0·75 and 1·57 with a mean of 1·04 (10 specimens), and the sheath is narrower than the preputium. A relatively short ephiphallus can be seen through the thin wall of the penis sheath (Text-fig. 12). The vagina is not everted as in *B. scalaris.*

REMARKS. The characteristics of the shell and the copulatory organ are constant in a large number of specimens, but as only a single population was found it can only be provisionally regarded as representing a new form within the *B. forskali* group. It is an interesting possibility that the population is a hybrid one between *scalaris* and *forskali*, as in other parts of their range these species are found together with no signs of interbreeding (Mandahl-Barth, 1957b).

If this does prove to be a distinct form of *Bulinus* there is sufficient resemblance between the shell and that figured by Bourguignat to justify the use of the name *fischerianus.* The type locality of *fischerianus* was not precisely defined but it probably lies on the northern plateau of Ethiopia or Eritrea as Lake Tana is given by Bacci (1951) as the locality of other material attributed to the same collector (Verreaux).

Germain (1921) and Haas (1936) regarded *Bulinus fischerianus, B. beccarii* and *B. cernicus* as synonyms of *B. forskali*, while Mandahl-Barth (1957b) considered *cernicus* to be a distinct species with *fischerianus* and *beccarii* tentatively included as synonyms. As Wright (1963b) has recognised *beccarii* to be a distinct species in Western Aden Protectorate it is necessary to consider the relationship between *beccarii* and *fischerianus.* The status of *fischerianus*, which is an older name than either *cernicus* or *beccarii* was not discussed by Paladilhe who compared *beccarii* only to Egyptian forms of *Bulinus.* Direct comparison between the descriptions and



FIGS. 25–29. Aperture length (ML) plotted against shell length (L), + =*Bulinus forskali* from 62 km. S. of Kombolchia ; · =*B. scalaris* from 4 km. N. of Gorgora. FIG. 26. Aperture length (ML) plotted against shell length (L), + =*B. forskali* from Lake Margherita ; · =*B. scalaris* from 47 km. N. of Medhanie Alem. FIG. 27. Number of whorls (Wh) plotted against shell length (L), + =*B. forskali* from 62 km. S. of Kombolchia ; o =*B. forskali* from 10 km. S. of Uachile Wells ; · =*B. scalaris* from 47 km. N. of Medhanie Alem. FIG. 28. Length of copulatory organ (PS+PP) plotted against shell length (L), + =*B. forskali* from Lake Margherita ; · =*B. scalaris* from 3 km. N. of Gorgora. FIG. 29. Shell diameter (D) plotted against umbilicus diameter (UD), + =*Gyraulus convexiusculus* from Tafwa, near Dahla, Western Aden Protectorate, collected and det. C. A. Wright ; · =*G. costulatus* from 1 km. S. of Debra Berhan.

figures of *fischerianus* and *beccarii* is hampered by the difference in size of the figured specimens, and one important feature distinguishing *beccarii*, the relatively large lowest whorl could be regarded as merely a juvenile character as the figured specimen of *beccarii* is only 4 mm. long. However, the manner of growth appears to be significantly different in the two forms, as at a length of 4 mm. *beccarii* has completed 4½ whorls, whereas at 8 mm. length, *fischerianus* consists of only 5 whorls.

Subfamily **PLANORBINAE**

PLANORBIS Müller

Planorbis planorbis parenzani Bacci

Planorbis (*Tropidiscus*) *planorbis parenzani* Bacci, 1940 : 456, pl. 1, fig. 1.

LOCALITY. Arussi : 5 km. approx. S. of Adamitullo (between Lake Zwai and Bulbulla River) (50).*

Shell (pl. 3, 15 and 16)

Largest specimen : D = 5·3 mm. ; UD = 2·3 mm. ; H = 2·0 mm. ; 4 whorls.

REMARKS. These specimens are similar to sub-fossil shells described by Bacci (1940) in the maximum individual size and the rate of widening of the whorl, but differ in being relatively thicker and possessing a less acute basal angulation. This difference is seen most clearly in the aperture which is far more rounded in the present specimens. The chief characteristic distinguishing *P. planorbis parenzani* from *P. planorbis philippi* Monterosato is the relatively acute basal angulation in the former. As this characteristic is not well defined in the present shells, which like Bacci's specimens were collected from the plain that formed part of an ancient bed of Lake Zwai, it is doubtful whether the separation of the two forms is justified.

DISTRIBUTION. No living specimens have been found of this *Planorbis* which appears to be closely related to the small forms of *Planorbis planorbis* that occur in N. Africa and the near East.

ANISUS Studer

Anisus natalensis (Krauss) species group

Anisus natalensis (Krauss)

Planorbis natalensis Krauss, 1848 : 83, pl. 5, fig. 9 ; ? *Planorbis natalensis ;* Blanford, 1870 ; *Gyraulus* (*Anisus*) *natalensis ;* Mandah-Barth in Ayad, 1956 ; *Anisus natalensis ;* Wright & Brown, 1962.

Planorbis abyssinicus Jickeli, 1874 : 215, pl. 7, figs. 21a–c ; Bourguignat, 1883 ; Pollonera, 1898 ; Germain, 1904 ; Neuville & Anthony, 1908 ; Connolly, 1928 ; *Planorbis abyssinicus* var. *gravieri* Germain, 1904 : 353.

LOCALITIES. Arussi : Lake Zwai, N.W. shore (30) ; 30–60 km. W. of Shashamanni on Soddu road, 4 samples (187). Begemeder : 66–97 km. N. of Gondar on Asmara road, 3 samples (220) ; Lake Tana at Gorgora (16). Choa : 22–318 km. N.E. of Addis Ababa on Asmara road, 5 samples (153) ; 32–185 km. W. of Ambo (50); Lake Wonji (15); 21 km. E. of Wolisso (21). Eritrea : 39 km. S. of Asmara on Gondar road (6) ; 8 and 38 km. N.W. of Asmara on Cheren road (145) ; 144 km. S. of Asmara on Addis Ababa road (193) ; 19 km. E. of Teramni on Decamere road (150). Harar: 43 and 46 km. on Carsa road from junction with Dire Dawa—Harar road (60). Kaffa : Between Kombi and Jimma, 4 samples (120) ; 4 km. W. of

Jimma on Bonga road (2) ; 34 km. N. of Jimma on Agarro road (3). Sidamo : Wondo (1) ; 30 and 45 km. south of Adolla (138) ; Lake Margherita (67). Tigre : Lake Ashangi, N.E. shore (10) ; 0·5 km. S. of Adowa on Gondar road (1). Wollo : Lake Haik, S. shore (50).

Shell

The majority of specimens resemble those from near Debra Markos described by Wright & Brown (1962), but there are relatively few shells in the present collection with as large and rounded an aperture as the shell illustrated in the earlier paper.

Largest shells : D = 7·0 mm. ; UD = 3·3 mm. ; H = 1·8 mm. (Lake Tana at Gorgora). D = 7·0 mm. ; UD = 3·5 mm. ; H = 1·8 mm. (Eritrea, 19 km. E. of Teramni).

Anatomy

Anatomical characteristics are similar to those previously described (Wright & Brown, loc. cit.). The anus opens near the tip of the pseudobranch, which is a simple lobe lacking any ridges. The ovotestis consists of up to 30 acini, which are arranged in two irregularly alternating rows. The spermathecal duct is stout, and may be wider than the vagina at the point of junction. There are up to 18 primary prostate gland lobes several of which may be subdivided. In many samples the copulatory organ is similar to that previously described, having the penis sheath slightly longer and about half as wide as the preputium, but in a few samples (e.g. Lake Zwai) the sheath is relatively shorter and narrower. The penis is similar to that of Debra Markos specimens in appearance, but a few specimens have now been observed in which there is some evidence that the cuticularised part of the penis is formed in a manner similar to that described by Hubendick (1958) for *Gyraulus*. The question of the homology of the terminal part of the penis of *A. natalensis* with the stylet of *Gyraulus* species can only be decided when the development of the penis has been studied in detail.

Remarks. Three differing accounts of the anatomy of *Anisus natalensis* have been recently published (Azevedo et al. 1961, Wright & Brown 1962, and Demian 1962). No specimens from the type locality (Umgeni Valley, Natal) appear to have been studied, but Wright & Brown examined specimens from Transvaal in which the penis was found to have a long cuticularised portion similar to that of Ethiopian specimens. As observations on the copulatory organ indicate that there may be more than one form of *Anisus* with this kind of penis in Ethiopia, the present specimens are provisionally referred to the *A. natalensis* species group. It should be noted that the specimen of *natalensis* illustrated by Krauss is far thinner with a more flattened aperture than in any Ethiopian specimen, or that illustrated by Azevedo et al. from Mozambique.

Specimens of *A. natalensis* from Tanganyika described by Demian possess a very small terminal penial stylet which is different to that of the Ethiopian and Transvaal specimens. A small stylet has also been described in *A. misellus* Morelet from Angola (Wright, 1963a). Another condition is described by Azevedo et al. (loc. cit.) in specimens from Mozambique which have a prostate gland consisting of a single lobe and a short penis with a terminal opening that lacks any stylet.

DISTRIBUTION. Snails of the *A. natalensis* group are widely distributed in Ethiopia and are often abundant ; a population was found at 2,890 (9,400 ft. approx.) in northern Choa. The presence of a similar penis in South African specimens indicates that this form has a widespread range in Africa.

GYRAULUS Charpentier

Gyraulus costulatus (Krauss)

Planorbis costulatus Krauss, 1848 : 83, pl. 5, fig. 8 ; *Planorbis costulatus* var. ; Jickeli, 1874 ; *Gyraulus costulatus ;* Mandahl-Barth in Ayad, 1956 ; Wright & Brown, 1962.
Planorbis stelzneri Martens (non Dohrn), 1869 : 212.
Planorbis aethiopicus Bourguignat, 1883 : 128 ; Jickeli, 1874 : pl. 7, fig. 23.
Caillaudia angulata Bourguignat, 1883 : 129 ; Jickeli, 1874 : pl. 7, fig. 22 ; Piersanti, 1941.
Planorbis gibbonsi Nelson, 1878 sensu Neuville & Anthony, 1908 ; Connolly, 1928.

LOCALITIES. Begemeder : 97 km. N. of Gondar on Asmara road (6). Choa : Between 11 km. N.E. of Addis Ababa and 1 km. S. of Debra Berhan on Asmara road, 5 samples (230) ; 32–59 km. N. of Addis Ababa on Debra Markos road, 4 samples (39) ; 10 km. W. of Ambo (8) ; 21 km. E. of Wolisso (2) ; tributaries of River Awash S. of Addis Ababa at Akaki, Dukem & Moggio (57). Sidamo : 17 and 30 km. S. of Adolla (70). Tigre : 0·5 km. S. of Adua on Gondar road (4). Wallaga : 22 km. W. of Guder on Lekemti road (22) ; 20 km. E. of Lekemti on Addis Ababa road (2). Wollo : 1 and 8·5 km. N. of Dessie (90).

Shell (pl. 3 ; 5 and 6, 10, 11)

The relationship between diameter and umbilicus diameter for part of a sample from 1 km. S. of Debra Berhan is shown in Text-fig. 29. The ratio D/UD ranges from 3·06 to 3·93, with a mean of 3·40 (20 shells).

The whorls are rounded in small shells, but the majority of medium and large specimens possess an angulation that is more or less acute and may bear a projecting fringe of periostracum. The angulation may be situated close to the underside of the shell, so that the lower surface is flattened, or nearer to the midline in which case the lower surface is rounded. In one sample (8 km. approx. N. of Dessie) the angulation is very slightly developed even in large specimens (pl. 3, 10 and 11). Transverse ribs of varying size are present, and may be covered with brown bands of periostracum. A very fine spiral sculpture is present in a few samples.

Four empty shells from Adowa (pl. 3, 5 and 6) have a rapidly widening whorl, and an acute angulation situated in the middle of the whorl. The height of the aperture is less than its width. A further specimen of this form, which resembles *Caillaudia angulata* Bourguignat, was obtained in Choa (59 km. N. of Addis Ababa, on the Debra Markos road).

Anatomy (Text-figs. 30, 31)

Some parts of the anatomy of *G. costulatus* have been previously described for specimens from Mozambique (Azevedo et al, 1957) and Angola (Wright, 1963a), but in neither of these accounts is the pneumostome region adequately described. In a well relaxed specimen (Text-fig. 30) the pulmonary siphon (PN) is a spout-like projection of the thickened ventral edge of the pneumostome, the left edge of which passes posteriorly for a short distance along the floor of the mantle cavity, overlying the rectum as a short median rectal ridge (MED, following the terminology of Schutte & Van Eeden, 1959). The pseudobranch lobe bears a dorsal lamella (UL), that corresponds to that described by Schutte & Van Eeden, but, with the free edge lying on the right side of the pseudobranch lobe, its position is reversed compared to that in *Biomphalaria pfeifferi*. As a result of this, the anus (A), which opens near the base of the attachment of the dorsal lamella, is hidden by this lamella in *G. costulatus*. From the free margin of the dorsal lamella at the level of the anus, a ridge passes posteriorly and overlies the rectum as the lateral rectal ridge (RR).

The genital organs (Text-fig. 31) are similar to those of specimens from Angola and Mozambique, but not more than three lobes of the prostate gland are present even in large specimens (Wright records 9 in Angolan specimens). The penial stylet resembles that described by Wright.

Radula

In all of 5 radulae (9 km. approx. N. of Dessie) the cusps of unworn central teeth are not short and rounded as figured by Azevedo et al. Lateral teeth have three cusps and towards the 12th tooth in each transverse row an additional cusp is developed lateral to the ectocone. The upper part of the 12th tooth is relatively broad compared to that of the preceding teeth and the subsequent marginal teeth bear 5 or 6 cusps, among which that representing the mesocone of the lateral teeth is usually the biggest.

REMARKS. Ethiopian *Gyraulus costulatus* can readily be distinguished from *Gyraulus* collected in Aden Protectorate and identified as *G. convexiusculus* Hutton by Wright (1963b). The whorl of the Aden specimens widens less rapidly than in *G. costulatus*, and the umbilicus is wider (Text-fig. 29) ; this difference in shell shape is reflected in the far more elongated genital system of *G. convexiusculus*.

There is considerable variation in shell shape but this does not lend itself to arrangement in subspecific categories as is possible for *G. costulatus* in Uganda and adjacent territories (Mandahl-Barth 1954). No Ethiopian specimens were collected from lakes which were the kind of habitat in which well defined forms were found by Mandahl-Barth.

A few specimens resembling *Caillaudia angulata* Bourguignat were obtained from two localities. As no other *Gyraulus* were found in these places, and no shells of similar shape are present in the other samples of *G. costulatus*, it is possible that Bourguignat's species is distinct from *G. costulatus*. The anatomy of the single living specimen that was obtained is similar to that of *G. costulatus*. *G. angulata* was described from one of Jickeli's figured specimens of *Planorbis costulatus* var. (Pl. 7, fig. 22), the other of which (pl. 7, fig. 23) was named *P. aethiopicus* by Bourguignat who considered it to be strikingly different to *P. costulatus* of Krauss. Krauss figured a shell that is unusually flattened with a carination and coarse ribs, whereas Jickeli's specimen is relatively thick with an almost evenly rounded whorl and finer ribs. The synonymy of the Ethiopian forms with *G. costulatus* cannot be established with certainty until large samples are examined from near the type locality in Natal.

Planorbis abyssinicus Jickeli is listed as a subspecies of *G. costulatus* by Bacci (1951), but careful examination of the description and figure of the shell shows that the species resembles *Anisus natalensis* far more closely.

Planorbis ehrenbergi Beck (=*P. cornu* Ehrenberg, nom. nud.) is recorded from near Addis Ababa by Neuville & Anthony (1908) with some reservation. This species appears to be a *Gyraulus* and is otherwise known from the Egyptian Nile. The shell (Roth, 1856, pl. 2, figs. 6–9) is not angulated, and the aperture is relatively rounded in a manner very similar to the specimen illustrated in pl. 3 (figs. 10, 11) of the present paper. If this is a valid species, it is likely as Neuville & Anthony remark, that it does occur in Ethiopia. The present specimens are referred to *G. costulatus*, pending the clearer definition of the forms of *Gyraulus* occurring in Africa, on both conchological and anatomical grounds.

DISTRIBUTION. *G. costulatus* is widely distributed in Ethiopia and is often abundant in small slow-flowing waters ; a population was found at an altitude of 2,800 m. (9,150 ft.). Further south in Africa this species has an extensive range that includes Natal and the Congo.

LENTORBIS Mandahl-Barth

Lentorbis junodi (Connolly)

Hippeutis junodi Conolly, 1922 : 121 ; *Segmentina* (*Hippeutis*) *junodi* Conolly, 1925 : 200, pl. 4, fig. 30 ; *Lentorbis junodi ;* Mandahl-Barth, 1954.

LOCALITY. Choa : 62 km. S. of Kombolchia (18).

Shell

The shells closely resemble the type series (B.M.N.H.) of which two specimens are illustrated by Wright (1963a), and conform to descriptions given by Mandahl-Barth (1954) and Azevedo et al (1961). In all the shells there is a spiral microsculpture of fine wavy lines which are much finer than the longitudinal striations mentioned by Azevedo et al (loc. cit.). The colour has been described by previous authors as red-brown to light orange, but the present specimens are very pale horn coloured, or almost colourless.

Largest specimen : D=4·2 mm.; H=1·6 mm.; 4½ whorls.

Anatomy (Text-figs. 32)

The structure and arrangement of the genital organs (Text-fig. 32) agrees with the description given by Mandahl-Barth (1954), except in respect of the prostate gland which bears a larger number of lobes (18 instead of 12) in the present material, the spermatheca which has a long instead of a short duct, and the penis which is not coiled in the upper part of the sheath. As described by Azevedo et al (loc. cit.) the lobes of the prostate appear to open into a separate prostatic duct, and the vas deferens opens at the tip of the penis. The ovotestis consists of approximately 20 acini arranged in two alternating rows.

REMARKS. There is a close resemblance between the type series of *L. junodi* and two of the original specimens of *L. benguelensis* (Dunker) apart from the presence of traces of septa in *junodi* already noted by Wright (1963a). This author contrasted the copulatory organ of his specimens of *L. benguelensis*, in which the sheath and preputium are nearly equal in length and width, with the copulatory organ of *L. junodi* in which the sheath is about twice as long and narrower than the preputium according to Azevedo et al (1961). These authors account of the copulatory organ of *L. junodi* is confirmed in the present specimens, but further anatomical study is desirable to establish the distinctness of these two species with certainty.

DISTRIBUTION. *Lentorbis* does not appear to have been previously recorded from Ethiopia. Mandahl-Barth (1954) drew attention to the great distance separating *L. junodi* in Uganda from the previously known range confined to Mozambique, and it seems likely that the apparently discontinuous range of *Lentorbis* merely reflects the ease with which specimens are overlooked.

SEGMENTORBIS Mandahl-Barth

Segmentorbis (Segmentorbis) angustus (Jickeli)

Segmentina angusta Jickeli, 1874 : 220, pl. 7, fig. 24 ; *Segmentina angusta? ;* Blair in Ayad, 1956 ; *Segmentorbis angustus ;* Mandahl-Barth, 1954.

LOCALITIES. Arussi : Lake Zwai, N.W. shore (1). Choa : 64 km. S. of Kombolchia on Addis Ababa road (1). Eritrea : 15 km. N.W. of Asmara on Cheren road (4) ; River Toquor near Mekerka village (4). Kaffa : 22 km. approx. W. of Assendabo on Jimma road (2) ; 34 km. N. of Jimma on Agarro road (2).

Shell

Two sets of septa are present in all the specimens obtained from the type locality (River Toquor, near Mekerka), and there are traces of a third set in one shell. Up to five basal septa are present in shells from other localities. All the specimens from near Mekerka have the centre of the upper surface slightly depressed, but in the specimen from Lake Zwai this surface is flat. Spiral sculpture that is finer and less regular than that of *L. junodi* is present on some shells.

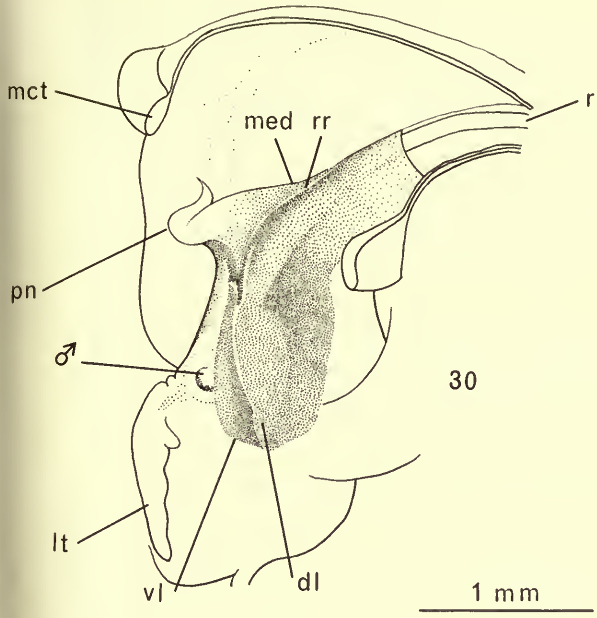
Largest shell : Lake Zwai) D=5·0 mm.; H=1·7 mm.; 4¾ whorls.

Anatomy (Text-fig. 33)

The pneumostome region is similar to that of *L. junodi* with the anus opening at the left edge of an anal lobe that lacks ridges.

The genital organs of a specimen from the type locality are illustrated in Text-fig. 33. There are between 20 and 30 slender acini, arranged in two alternating rows, composing the ovotestis. An extremely thin part of the hermaphrodite duct precedes the seminal vesicle region, which is large in comparison to that of *L. junodi*, and bears filamentous processes. Similar genital organs are present in a specimen from Kaffa Province, which has even longer filamentous processes from the seminal vesicle region and about 40 acini in the ovotestis.

REMARKS. There is a close resemblance between the shells of specimens from near Mekerka and those described by Jickeli, and although this author does not mention internal septa in his description, at least one septum is visible on the basal surface near the aperture in pl. 7, fig. 24c. Between 1 and 5 sets of septa have been recorded in specimens of *S. angustus* from Uganda (Mandahl-Barth, 1954) and Mozambique (Azevedo et al. 1961).



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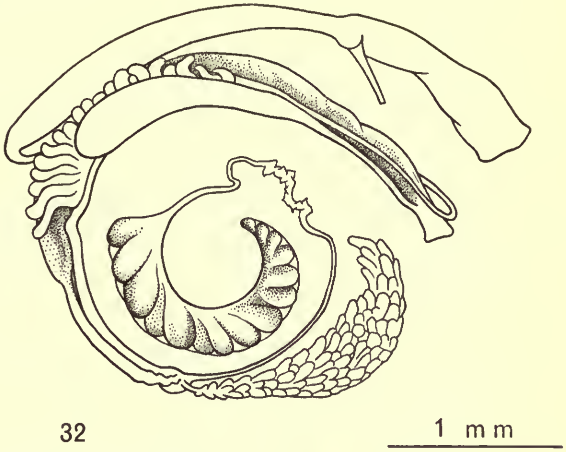

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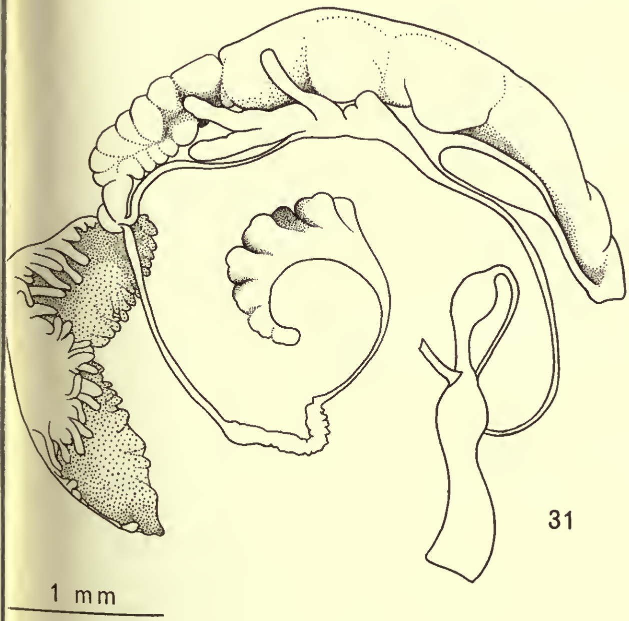

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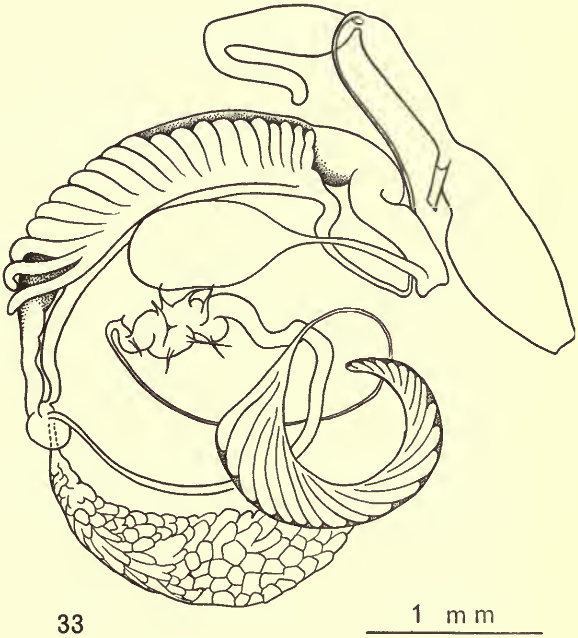


33

Figs. 30, 31. *Gyraulus costulatus* from 1 km. S. of Debra Berhan. Fig. 30. Anterior part of animal viewed from left side, mantle cut on left side and raised to expose pulmonary siphon and pseudobranch. Fig. 31. Genital organs.

Fig. 32. *Lentorbis junodi* from 62 km. S. of Kombolchia, genital organs. Fig. 33. *Segmentorbis angustus* from River Toquor near Mekerka, genital organs.

According to these authors the duct of the spermatheca is approximately four times as long as the sac. The kind of spermatheca present in Ethiopian specimens is described by Mandahl-Barth for *S. planodiscus* (Melville & Ponsonby). However, as noted by this author, the sexual condition of the individual snail may effect the shape of the spermatheca and it is possible that the same factor accounts for the differences between the present specimens and those described by Azevedo et al (loc. cit.). These differences lie in the number of acini in the ovotestis, the number and arrangement of the lobes in the prostate (only four 3-branched lobes were observed in material from Mozambique), and the greater size of the seminal vesicle region in the Ethiopian specimens.

DISTRIBUTION. Like the preceding species, *S. angustus* is easily overlooked, and is probably more widely distributed and abundant in Ethiopia than the records indicate. The species has a wide distribution in Africa, extending at least as far south as Mozambique.

Segmentorbis (Acutorbis) kanisaensis (Preston)

Segmentina kanisaensis Preston, 1914 : 265, pl. 18, figs. 17–19 ; *Segmentorbis kanisaensis ;* Mandahl-Barth, 1954.

LOCALITY. Choa : 62 km. S. of Kombolchia (1).

REMARKS. The occurrence of this species in Ethiopia is to be expected as it was originally described from the Nile at Kanisa and has a wide range extending to Natal (Connolly, 1939) and Angola (Wright, 1963a).

BIOMPHALARIA Preston

Biomphalaria sudanica species group

Biomphalaria sudanica (Martens)

Planorbis sudanicus Martens, 1870 : 35.

Planorbula alexandrina (non *Planorbis alexandrinus* Ehrenberg, 1831) Pilsbry & Bequaert, 1927 : 131.

Afroplanorbis boissyi tanganikanus (Bourguignat, 1888) Bacci, 1941.

Planorbis bozasi De Rochebrune & Germain, 1904 a : 141 ; 1904 b : pl. 1, figs. 2–4.

Planorbis abyssinicus (non *Planorbis abyssinicus* Jickeli, 1874) Piersanti, 1941 : fig. 37.

LOCALITIES. Arussi : Lake Zwai, N.W. shore (78) ; Lake Abyata, E. shore (15)*. Sidamo : Lake Awasa, E. shore (2)* ; Lake Margherita, E. shore (34).

Shell (Pl. 3, figs. 7–9, 12–14, Text-fig. 34)

The shells from Lakes Zwai, Awasa and Margherita have a flattened upper surface with a blunt angulation at the periphery. Beneath the angulation the surface of the whorl is more or less flattened, and there is a basal angulation close to the suture. The aperture is markedly asymmetrical in outline, being wider than it is high in the majority of specimens. The range and mean of ratio UD/H for shells between 9·0 and 10·9 mm. diameter are shown in Text-fig. 34. Coarse irregular transverse ridges are present, and where these are crossed by spiral grooves a nodular microsculpture is formed.

Largest shell (Lake Zwai) : D=15 mm.; UD=5·7 mm. ; H=4·7 mm. ; $5\frac{1}{2}$ whorls. (Lake Abyata) : D=11·8 mm.; UD=3·74 mm.; H=4·4 mm.; $5\frac{1}{2}+$ whorls.

In the Lake Abyata specimens (pl. 3, figs. 12–14) the upper surface of the shell is slightly curved and the peripheral angulation is not so sharp. The width of the whorl does not increase so rapidly, the shape in cross section is almost symmetrical, so that the aperture is relatively small and almost as high as it is wide. The range and mean of ratio UD/H are included in Text-fig. 34.

Anatomy

Animals were obtained only from Lakes Zwai and Margherita. The penis sheath is a little longer or shorter than the preputium ; PS/PP in 10 specimens from Lake Zwai ranges from 0·78–1·04 mm.

Radula

The cusps of the lateral teeth are triangular (Lake Awasa, 12 radulae), or somewhat arrow-head shaped (Lake Margherita, 1 radula). In marginal teeth where the ectocone is present it is usually a single cusp, but this may have a serrated edge and up to three small cusps have been observed.

Remarks. It will be seen in Text-fig. 34 that although the three samples of *B. sudanica* lie at the upper limit of the variation of UD/H, there is no marked discontinuity from the series of samples of *B. pfeifferi rueppelli*, one of which (No. 26) has a greater mean ratio UD/H than the sample of *B. sudanica* from Lake Abyata (No. 25). A large number of radulae are available only for *B. sudanica* from Lake Zwai, and although a single ectocone cusp is more frequently present on the marginal teeth in these specimens, there are no consistent differences to the radulae of the population of *rueppelli* mentioned above, or another (No. 24) which also has a high mean ratio UD/H. Both these populations are from near the floor of the Rift Valley close to the River Awash, so that although in general appearance they resemble the plateau form of *rueppelli*, it is possible that some genetic exchange has taken place with the lake populations of *B. sudanica*.

Pilsbry & Bequaert (1927, p. 131) state that they have seen specimens of *Planorbula alexandrina* from Lake Abaja (Lake Margherita), and it is of interest that the radula of a specimen from this lake has cusps approaching the arrow-head shapecharacteristic of the *Biomphalaria alexandrina* species group (Mandahl-Barth, 1957a). The copulatory organ resembles that of *B. sudanica*, having the penis sheath shorter or not much longer than the preputium.

Planorbis bozasi described from Lake Shala closely resembles *B. sudanica* from Lake Zwai. No *Biomphalaria* were found in Lake Shala during the recent expedition and it is unlikely that living molluscs occur in the lake at the present time because of the high alkalinity.

It is evident from the figure and the dimensions (diameter=14·5 mm.) that "*Planorbis abyssinicus*" recorded by Piersanti from Lake Stephanie is not Jickeli's species, which resembles *Anisus natalensis*, but is probably *B. sudanica*.

Distribution. *Biomphalaria sudanica* is restricted to certain lakes in the southern part of the Ethiopian Rift Valley ; it occurs in Sudan, Uganda, Congo and N. Rhodesia, and has recently been found in Ghana (Mandahl-Barth, pers. comm.).

Biomphalaria pfeifferi species group

Biomphalaria pfeifferi rueppelli (Dunker)

Planorbis rüppellii Dunker, 1848 : 42 ; Martini & Chemnitz, 1856 : 41, pl. 5, figs. 10–12 ; Martens, 1869 ; Blanford, 1870 ; Morelet, 1872 ; Jickeli, 1874 ; Nevill, 1878 ; Bourguignat, 1883 ; Pollonera, 1898 ; De Rochebrune & Germain, 1904 ; Neuville & Anthony, 1908 ; Connolly, 1928 ; Giovannola, 1939 ; *Planorbis* (*Biomphalaria*) *rüppellii ;* Piersanti, 1940 ; Piersanti, 1941 ; *Biomphalaria rüppellii ;* Mandahl-Barth in Ayad, 1956 ; *Biomphalaria rueppelli ;* Wright & Brown, 1962.

Planorbula alexandrina (non *Planorbis alexandrinus* Ehrenberg, 1831) Pollonera, 1898 : 11.

Planorbis biossyi (non *Planorbis biossyi* Potiez & Michaud, 1838) Jickeli, 1874 : 213 ; Pollonera, 1898 : 11 ; Giovannola, 1937 : 158 ; *Planorbis biossyi* var. *asmarica* Satta, 1936 : 193.

Planorbis adowensis Bourguignat, 1879 : 11 ; 1888 : pl. 1, figs. 1–4 ; Germain 1904 ; Neuville & Anthony, 1906 ; Germain, 1921 ; Giovannola, 1939 ; *Planorbis herbini* var. *adowensis ;* Pollonera, 1898 ; *Biomphalaria adowensis ;* Bacci, 1941.

Planorbis herbini Bourguignat, 1883 : 101 (Jickeli, 1874 : pl. 7, fig. 18) ; Pollonera, 1898 ; Germain, 1904 ; Connolly, 1928.

Planorbis cecchii Pollonera, 1887 : 2.

Planorbis bridouxi (non *Planorbis bridouxianus* Bourguignat, 1890) Neuville & Anthony, 1908 : 253, fig. 2 ; Germain, 1931 : 366.

Planorbula boccardi Pollonera, 1898 : 11, figs. 22–25.

LOCALITIES. Arussi : 5 km. approx. S. of Adamitullo near Bulbulla River (1)* ; River Awash S. of Nazareth (5) ; 1 km. S. of River Awash on Asella Road (150). Begemeder : 3 and 8 km. N. of Gorgora on Gondar Road (14) ; 5 and 66 km. N. of Gondar on Asmara road (24) ; 1, 14 and 115 km. N. of Medhamie Alem on Asmara road (115). Choa : Lake Hora (23)* ; Lake Bishoftu (10) ; S. of Akaki (80) ; N. of Dukem, 2 samples (135) ; Awash river on Addis Ababa–Wolisso road (60) ; 21 km. E. and 30 km. W. of Wolisso (65) ; 1–10 km. W. of Ambo, 4 samples (300) ; 32–177 km. N. of Addis Ababa on Debra Markos road, 5 samples (460) ; 11–51 km. N. of Addis Ababa on Asmara road, 4 samples (540) ; 222 (Robi village) and 264 km. N. of Addis Ababa on Asmara road (250) ; 98 km. N. of Robi village on Asmara road (52). Eritrea : 22–83 km. S. of Asmara on Gondar road, 6 samples (280) ; 2 km. W. of Adi Ugri on Arezza road (8) ; 3 km. E. of Teramni on Decamere road (6) ; 66 and 70 km. S. of Asmara on Addis Ababa road (225) ; River Toquor near Mekerka village (214). Harar : 10 km. W. of Harar on Dire Dawa road (110) ; 9 km. E. of Harar on Jijiga road (38) ; 8 km. E. of Aramyia village (8) ; 46 km. on Carsa road from junction with Dire Dawa–Harar road (300) and 3 km. approx. W. of junction (10). Kaffa : 9 km. W. of Kombi–22 km. W. of Assendabo on Addis Ababa–Jimma road, 8 samples (180) ; 4 and 14 km. W. of Jimma on Bonga road (190) ; 34 and 38 km. N. of Jimma on Agarro road (130). Sidamo : Storage dams at Neghelli, 3 samples (238). Tigre : 0·5 km. S. of Adowa on Gondar road (180)*; 222 km. S. of Asmara on Addis Ababa road (7). Wallaga : 9 km. W. of Guder on Lekemti road (8). Wallo : 1 km. within N. boundary of Dessie on Asmara road and 30 km. N. of town (280) ; 0·5 km. W. of Kombolchia on Dessie road (14) ; 10 km. approx. E. of Kombolchia on Batei road (400) ; 1 km. W. of Batei N. of Kombolchia road (169) ; 26 km. S. of Kombolchia on Addis Ababa road (30).

Shell

The shells are generally thicker, with a narrower umbilicus and less flattened upper surface than in *B. sudanica.* The largest specimen is 15·8 mm. in diameter and consists of 4⅞ whorls, i.e. approximately one whorl less than in a *sudanica* shell of the same size. A spiral microsculpture consisting of rows of short ridges and nodules is present on the lower and upper surfaces of some specimens in the majority of samples. The relationship between D, UD, and H was found to vary in the same sample with the size of the shell, i.e., UD/H tended to increase with D as in two samples from near Debra Markos, Gojjam Province, described by Wright & Brown (1962). The mean and range of the ratio UD/H for 25 samples is shown in Text-fig. 34 ; a limited size group of D has been selected in order to minimise the effect of variance of UD/H with D, on the variance between different samples.

Anatomy

Some details of the gross anatomy of *B. pfeifferi rueppelli* are given by Wright & Brown (loc. cit.), and the only difference observed in the present material is that the internal muscle pillars of the preputium are variable in their relative size instead of being constantly asymmetrical.

The proportions of the copulatory organ of a sample from 10 km. W. of Harar (Text-fig. 34, 3) with a narrowly umbilicate shell are : mean PS/PP = 0·83 ; range 0·59–1·00 (10 specimens). In a samples from 34 km. N. of Jimma (Text-fig. 34, 23) with a widely umbilicate shell : mean PS/PP = 0·80 ; range 0·73–1·16 (10 specimens).

Radula

As was the case in specimens from near Debra Markos the degree of subdivision of the ectocone of the marginal teeth (mistakenly called lateral teeth, Wright & Brown loc. cit., p. 297, l. 34) is variable. Four cusps are present in 4 out of 15 radulae examined, but in 13 radulae at least some marginal teeth have an undivided ectocone.

REMARKS. There are such conspicuous differences in shell shape between many of the populations of *B. pfeifferi rueppelli* in Ethiopia that the existence of many synonymous records is not surprising. The range of variation of UD/H (Text-fig. 34) of several samples overlaps only slightly or not at all, but there is a more or less continuous variation in the mean ratio UD/H between the most narrowly and the most widely umbilicate populations. No differences have yet been observed in the anatomy or radulae of samples representing the extreme limits of this variation, and there appears to be no justification for recognising more than a single form of the *B. pfeifferi* group in the plateau region of Ethiopia. Mandahl-Barth (1960) has proposed that the use of subspecies in this group should be abandoned, but it seems useful to retain a subspecific category *rueppelli* for the *B. pfeifferi* of the Ethiopian Plateau (and possibly also the Arabian Peninsula), where a higher proportion of narrowly umbilicate populations reaching a small maximum size seems to occur in comparison to the rest of the range of the species.

After examining the original specimens, Bacci (1943) concluded that *Planorbula alexandrina* and *P. boccardi* recorded from Eritrea by Pollonera were not significantly different. The figures of the latter species represent a frequently occurring form of *rueppelli*. It is highly probable that the two single shells of *P. boissyi* recorded by Jickeli and Pollonera are relatively widely umbilicate shells of *rueppelli*, to which species Giovannola (1939) refers his own record (1937) of *P. boissyi* and that of Satta. As pointed out by Mandahl-Barth (1957a), *P. herbini* and *P. cecchii* are probably narrowly umbilicate and juvenile shells respectively of *rueppelli*, but with regard to the occurrence of *B. sudanica* in the Rift Valley of Ethiopia it now appears that *P. bozasi* belongs to this species. The specimens of *P. bridouxi* illustrated by Neuville & Anthony represent a narrowly umbilicate *rueppelli* with a widely flared aperture.

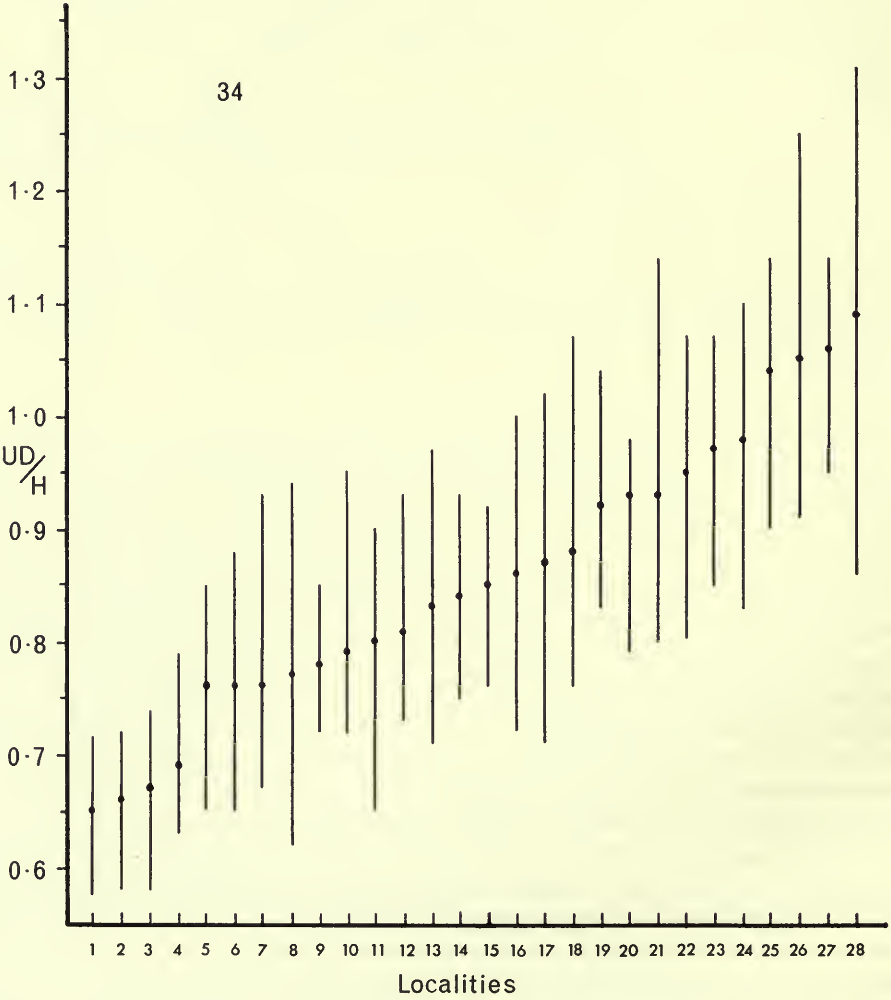


FIG. 34. Range and mean of the ratio UD/H (umbilicus diameter/height) of *Biomphalaria* shells between 9·0 and 10·9 mm. diameter. Localities 1–24 and 26 *B. pfeifferi rueppelli*, 25, 27 and 28 *B. sudanica*.

List of localities

1. Eritrea ; 32 km. W. of Asmara on Cheren road.
2. Choa ; Lake Hora.
3. Harar ; 10 km. W. of Harar.
4. Tigre ; 0·5 km. S. of Adowa.
5. Wallo ; 1 km. N. of Dessie boundary.
6. Harar ; 46 km. on Carsa road.
7. Eritrea ; 83 km. S. of Asmara on Gondar road.
8. Eritrea ; River Toquor near Mekerka.
9. Choa ; 32 km. N. of Addis Ababa on Debra Markos road.
10. Eritrea ; 101 km. S. of Asmara on Addis Ababa road.
11. Eritrea ; 39 km. S. of Asmara on Gondar road.
12. Harar ; 9 km. E. of Harar.
13. Choa ; 35 km. N. of Addis Ababa on Asmara road.
14. Choa ; 10 km. W of Ambo on Lekemti road.
15. Kaffa ; 26 km. W. of Sokuru on Jimma road.
16. Sidamo ; army barracks Neghelli.
17. Choa ; 59 km. N. of Addis Ababa on Debra Markos road.
18. Choa ; 4 km. W. of Ambo on Lekemti road.
19. Choa; 42 km. N. of Robi on Asmara road.
20. Kaffa ; 9 km. W. of Assendabo on Jimma road.
21. Begemeder ; 1 km. N. of Medhanie Alem on Asmara road.
22. Begemeder ; 14 km. N. of Medhanie Alem on Asmara road.
23. Kaffa ; 34 km. N. of Jimma on Agarro road.
24. Choa ; outflow below Koka Dam.
25. Arussi ; Lake Abyata.
26. Arussi ; 1 km. S. of River Awash on Asella road.
27. Sidamo ; Lake Margherita.
28. Arussi ; Lake Zwai.

Particular attention must be given to *P. adowensis* as this form has been frequently discussed in the literature. Bourguignat states (1883, p. 101) that *P. adowensis* is " remarquable par sa forme globuleuse, et par la rapidité de sa croissance spirale ", but the specimen illustrated (1888) from Lake Tanganyika shows these characteristics to a lesser degree than does the shell illustrated as *P. bridouxianus*, which closely resembles the specimens from near Adowa in the present collection and that illustrated by Mandahl-Barth (1957a). Germain (1904) accepts that both *bridouxianus* and *adowensis* are narrowly umbilicate forms, traces a continuous gradation between *sudanica* and *bridouxianus*, and suggests geographical ranges for some of the intermediate forms. Giovannola (1939) also finds a geographical pattern in distribution of shell shape, contrasting *B. rueppelli* of Eritrea with the relatively narrowly umbilicate *P. adowensis* occurring in the vicinity of Harar. However, Neuville & Anthony (1908) do not recognise *adowensis* as a distinct species and draw attention to the great variation occurring in a limited area and the existence of mixed populations. The present collection supports this view, also held by Mandahl-Barth (loc. cit.), that there is no clear geographical separation in the ranges of the two forms, and it appears likely that narrowly umbilicate shells occur in all parts of the range of *B. pf. rueppelli*. It is also evident that when a large number of populations are considered there is a gradation between the extremes of shell shape. However, individual populations may exhibit only a limited part of the range of shell shape, and this may also be so in groups of populations, as shown by the present samples from near Harar which are all relatively narrowly umbilicate as was observed by Giovannola. Specimens of "*adowensis*" from near Adowa were found to have the penis sheath much shorter than that of *rueppelli* by Mandahl-Barth. No marked difference was found between the copulatory organs of two samples representing the extremes of shell shape in the present collection (see Anatomy, above).

DISTRIBUTION. The range of *B. pfeifferi* extends over most of Africa south of the Sahara ; *B. rueppelli* has been recorded from many parts of this range outside Ethiopia but it is here concluded that only the *Biomphalaria* of the Ethiopian plateau, possibly together with those of the Arabian Peninsula, merit recognition as the subspecies *B. pfeifferi rueppelli*.

Family **FERRISSIIDAE**

BURNUPIA Walker

Burnupia caffra (Krauss)

Ancylus caffer Krauss, 1848 : 70, pl. 4, fig. 13 ; *Burnupia caffra ;* Walker, 1923 ; *Burnupia sp.* cf. *caffra ;* Brown, 1961.

Burnupia (*? abyssinica* Jickeli) ; Mandahl-Barth in Ayad, 1956.

LOCALITIES. Begemeder : 8 km. N. of Gorgora (30). Choa : 11 km. and 67 km. N. of Addis Ababa on Asmara road (47) ; 36 km. and 59 km. N. of Addis Ababa on Debra Markos road (12) ; 32 km. W. of Wolisso (2). Sidamo ; 17 km. and 30 km. S. of Adolla (45).

Shell

The shells resemble a small sample from Addis Ababa (Brown, 1961), in possessing a well developed apex that is turned to the right and situated in the posterior third of the shell. Shell shape varies considerably in the larger samples that have now been obtained ; the extreme values of the ratio H/L in the sample from Begemeder are 0·38 and 0·48. The shape of the shell base also varies within samples, it may be an evenly rounded broad oval, or narrow and irregularly flattened. Radial sculpture may be hardly detectable and confined to the edge of the shell, or well developed over much of the surface and visible at a relatively low magnification (× 10).

Anatomy (Text-fig. 16)

The pseudobranch (fig. 16) is divided into basal and upper lamellae, each of which may be folded transversely. The rectum passes through the posterior part of the basal lamella and the anus is not covered by the upper lamella.

The genital organs are similar to those described by Brown (1961). Characteristic features are, the few large lobes of the ovotestis, the absence of protuberances on the seminal vesicle region of the hermaphrodite duct, and the long lobes of the prostate gland. Larger specimens than those previously available have now been dissected. Up to 11 terminal lobes are present in the ovotestis (8 were previously described), and two additional lobes are sometimes present in the prostate gland giving a total of 10 terminal lobes. A dilatation of the vas deferens, preceding the junction with the penis sheath, has been observed in all specimens. All of 20 specimens dissected are euphallic.

The "carrefour" Brown (loc. cit.) situated at the base of the albumen gland duct proximal to the junction between the hermaphrodite duct, uterus and vas deferens, appears to correspond to the "fertilisation sac" in *Ancylus fluviatilis* (Duncan, 1960).

Radula (Text-fig. 37)

The central teeth are bicuspid. Inner lateral teeth have three large cusps and a small additional lateral cusp that increases in size towards the radula margin. Marginal teeth bear up to six small sharp cusps.

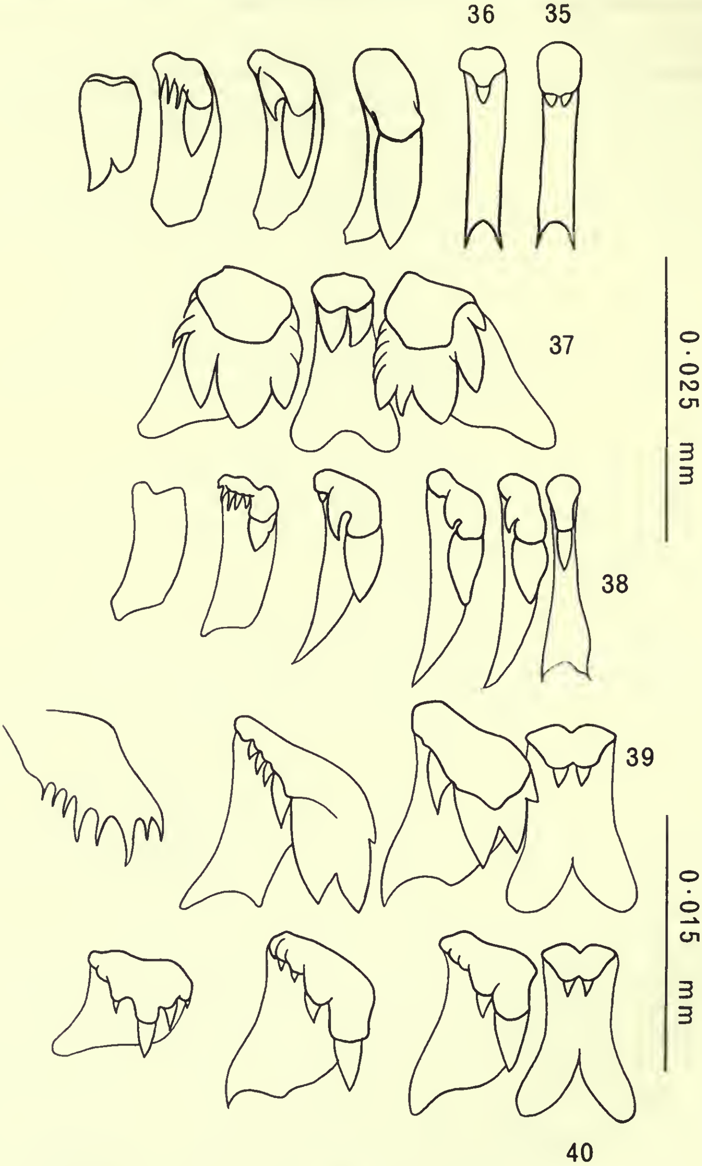
A radula from the Begemeder sample is unusual (Text-fig. 37) in having asymmetrical cusps on the central tooth, relatively large additional ectocones on the lateral teeth and bicuspid endocones on the first lateral teeth of one side. Grooves on the endocones of the lateral teeth are particularly marked in all the radulae seen of this sample.

REMARKS. In the larger samples the extent of variation is such that selected shells from each sample could be considered to belong to different species. As it is likely that many of the existing specific diagnoses within the genus *Burnupia* are founded on trivial differences in shell shape and ornamentation, the *Burnupia* in this collection are regarded as a single form.

Connolly (1939) gives the range of *B. caffra* as Natal and Cape Province, and the species is recorded from the Congo by Pilsbry and Bequaert (1927). The occurrence of similar specimens in Ethiopia suggests that *B. caffra* has a very wide range in Africa. It is also likely, considering the variation present in the Ethiopian samples, that the mixed populations mentioned by Pilsbry & Bequaert containing *B. caffra* and other species of *Burnupia* were composed of only a single form. However, it is remarkable that shells similar to *caffra* have not been found in East Africa; specimens figured by Mandahl-Barth (1954) as *B. stuhlmanni* (Martens, 1897), and *B. crassistriata* (Preston, 1911), differ clearly from the Ethiopian specimens, as do the paratypes of *B. kempi* (Preston, 1912, B.M.N.H.).

Two species of *Ancylus* described by Jickeli (1874) from a locality near Asmara, Eritrea, have been regarded as closely related to *Ancylus fluviatilis* (Müller) by Walker (1914), but Mandahl-Barth (in Ayad, 1956) raises the question that one of these species may be *Burnupia* by identifying specimens from near Asmara and Addis Ababa as *Burnupia ? abyssinica* (Jickeli). This record was unfortunately overlooked by Brown (1961) but Dr. Mandahl-Barth now considers that these specimens are "true *Ancylus*" (in litt.). As the specimens figured by Jickeli have the apex turned to the right far less acutely than do any Ethiopian *Burnupia*, and as no specimens of this genus were found in Eritrea during the recent expedition it is almost certain that Jickeli's species is not a *Burnupia*.

DISTRIBUTION. *B. caffra* appears to have a widespread range on the Ethiopian plateau N.W. of the Rift Valley, and also occurs at similar altitudes on the S.E. side of this valley. This species does not appear to have been recorded from the surrounding parts of N.E. Africa, but it probably has an extensive range as it was originally described from Natal and has been recorded in the Congo.



Figs. 35–40. Radula teeth. Figs. 35, 36. *Ancylus fluviatilis*. Fig. 35. 10 km. N. of Debra. Berhan, central. Fig. 36. River Toquor near Mekerka, central, 3, 29, 31 and 38. Fig. 37. *Burnupia caffra* from 8 km. N. of Gorgora, 1, central, 1. Fig. 38. *Ancylus* sp. from 15 km. N. of Dilla, central, 1, 3, 14, 23 and 27. Fig. 39. *Ferrissia clessiniana* ? from 17 km. S. of Adolla, central, 1, 8 and 16. Fig. 40. *Ferrissia isseli* ? from 89 km. W. of Guder, central, 1, 8 and 16.

FERRISSIA Walker[1]

Ferrissia clessiniana (Jickeli)?

Ancylus clessinianus Jickeli, 1882 : 366 ; *Ferrissia clessiniana ;* Walker, 1914 : figs. 9–11.
Ancylus sp. Blanford, 1870.

LOCALITIES. Arussi : 55 km. S. of River Awash on Asella road (45). Choa : 93 km. W. of Addis Ababa on Jimma road (1). Harar : 46 km. on Carsa road from Junction with Dire Dawa–Harar road (12). Sidamo : 4 km. S. of Wondo on Dilla road (30) ; 60 km. S. of Argereselam on Neghelli road (2) ; 17 km. S. of Adolla on Neghelli road (20).

Shell

The outline of the base is relatively narrow, wider in front than behind and more or less straight-sided (Text-figs. 46, 47). In one sample from Sidamo (S. of River Awash on Asella road) there is a gradation between this shape and an irregular oval outline. The apex is situated to the right of the longitudinal axis at about two-thirds of the longest dimension from the anterior margin ; in 10 shells this distance varies between 0·66 and 0·75 of the total length. The anterior surface is convex and the posterior surface concave ; the sides are almost flat and concave near the margin. Radial sculpture is absent except on the apex, where fine ribs are visible at a magnification of ×50. None of the specimens has a septum.

In two of the samples an unusually large size for *Ferrissia* in Africa is reached.

Largest shell (Sidamo, 17 km. S. of Adolla) : 4·3 mm. ; W = 2·5 mm. ; H = 1·2 mm. Sidamo : S. of River Awash : L = 5·2 mm. ; W = 3·7 mm. ; H = 1·7 mm.

Anatomy

All 10 specimens dissected are aphallic.

Radula (Text-fig. 39)

The central tooth is bicuspid. Three or four cusps are present on the median lateral teeth, and additional small cusps are developed on the lateral sides of the teeth towards the margin of the radula. The marginal teeth bear about 8 slender cusps that are nearly equal in size.

REMARKS. Four specimens recorded as *Ancylus sp.* by Blanford from near Mai Wahiz in Tigre Province appear to be the only *Ferrissia* previously collected in Ethiopia. Blanford compares these specimens to the Indian species *A. verruca* Benson, and they are considered to be a *Ferrissia* by Walker (1914) and Gwatkin (in Walker, loc. cit.).

The present specimens resemble *F. clessiniana* (Jickeli), originally described from near Alexandria, in the large individual maximum size and elongated basal outline ; other species of *Ferrissia* known to occur in Egypt (figured by Walker, loc. cit.) have a distinctly more rounded outline.

As all the specimens of *F. clessiniana?* were collected from submerged vegetation, including narrow stems and grasses, the possibility that their elongated shape may be partly due to the influence of the substratum should be considered. However, specimens collected by Dr. C. A. Wright at Tafwa, near Dhala (Western Aden Protectorate) from stones also have an elongated shape similar to that of *F. clessiniana*. There are consistent differences between the radulae of *F. clessiniana?* and the *Ferrissia* described below which has a rounded outline.

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[1] The genus *Ferrissia* is here used in accordance with past usage, but it is probable that true *Ferrissia* do not occur in Africa (see Introduction).

Distribution. *F. clessiniana?* appears to be widely distributed in the southern half of Ethiopia, occurring in streams containing thick vegetation.

Ferrissia isseli (Bourguignat)?

Ancylus isseli Bourguignat, 1866 : 214, pl. 33, figs. 13–18 ; *Ferrissia isseli* ; Walker, 1914.

Locality. Wallaga : 89 km. W. of Guder (22).

Shell (Text-fig. 45)

The outline of the base is ovate and more or less symmetrical, with the sides not straight for more than a short distance. The apex is blunt and rounded, situated slightly to the right of the longitudinal axis at about two-thirds of the longest dimension from the anterior margin. This distance varies in 10 shells between 0·64 and 0·73 of the total length. The anterior surface is gently convex and the posterior surface slightly concave or nearly straight. Lateral surfaces are slightly convex and not at all flared towards the margin as in the preceding species. Radial sculpture consists of very fine ribs confined to the apex. None of the specimens has a septum.

Largest shell : L = 3·2 mm. ; W = 2·3 mm. ; H = 1·5 mm.

Anatomy

All of the 10 specimens dissected are aphallic.

Radula (Text-fig. 40)

As in the preceding species the central tooth is bicuspid, but the shape of the upper parts of the lateral and marginal teeth, and the arrangement of the cusps is conspicuously different. The median side of the upper part of each lateral tooth is elongated and bears one large cusp (which may represent the fused ectocone and mesocone), that is set apart from the other cusps. There is relatively little change in the form of the teeth until close to the margin of the radula. Marginal teeth bear 4–5 widely spaced cusps of unequal size.

Remarks. The shells are relatively higher than those of the *Ferrissia* species described by Mandahl-Barth (1954), and resemble the shells from Alexandria identified as *F. isseli* and *F. pallaryi* by Walker (1914). As *F. pallaryi* was described from a sample of only three specimens, it is preferable to refer the Ethiopian specimens tentatively to the older name.

The broader basal outline of *F. isseli?* compared to that of *F. clessiniana?* could be attributed to the fact that all specimens of the former species were collected from stones. However, the radulae provide strong evidence that the two forms are distinct.

Family **ANCYLIDAE**

ANCYLUS Müller

Ancylus fluviatilis species group

Ancylus fluviatilis Müller

Ancylus fluviatilis Müller, 1774 : 201 ; Blanford, 1870.

Ancylus abyssinicus Jickeli, 1874 : 223, pl. 7, figs. 27 & 28 ; Bourguignat, 1883 ; Pollonera, 1898 ; De Rochebrune & Germain, 1904 ; *Pseudancylus abyssinicus ;* Connolly, 1941.

Ancylus hamacenicus Bourguignat, 1883 : 84, (= *A. compressus* Jickeli, nom. nud. 1874, pl. 7, fig. 26).

LOCALITIES. Begemeder : 5 km. and 45 km. N. of Gondar on Asmara road (6) and (78). Choa : 10 km. N. of Debra Berhan on Asmara road (4) ; 47 km. N. of Addis Ababa on Debra Markos road (2). Eritrea : 18 km. W. of Asmara on Cheren road (18) ; River Toquor near Mekerka village (55). Tigre : 222 km. S. of Asmara on Addis Ababa road (20).

Shell (Text-figs. 41–43)

There is great variation in the shape of the shell base, the relative proportions of length and height, and the shape of the apex. In a series of shells from the River Toquor near Mekerka, Eritrea (Text-fig. 41), the ratio W/L varies between 0·74 and 0·83, and H/L between 0·37 and 0·51. In the Tigre sample the apices are blunter, and one shell is almost circular in outline (Text-fig. 42). The shells from 30 km. N. of Gondar are characterised by very large curved apices, which overhang the posterior margin (Text-fig. 43).

The apex is sculptured with a variable number of radial ribs, that are coarse in comparison with those of the succeeding species. A few ribs (primary ribs) extend over the rim of the apical depression into the hollow of the depression, and additional ribs are developed in increasing numbers towards the periphery of the shell. On the apex primary ribs are usually larger than later formed ribs, but a short distance from the apex all ribs are of similar size, and near the periphery the radial sculpture consists of fine wavy ridges. In some shells the sculpture does not extend beyond the ridge marking the end of the first growth stage. Fine circular sculpture connects the primary ribs on the apex, and coarser more or less regular circular ridges are present on the rest of the shell surface. Shells differ in the number and relative size of the primary ribs, and in the rate at which later formed ribs are intercalated between them. In some shells approximately 40 ribs are present in the vicinity of the apical depression, but in others a smaller number (15 or less) of larger ribs is present. Each sample has a more or less distinctive type of radial sculpture ; both the extreme forms described above are present in the Mekerka sample, although the form with large primary ribs is the more frequent.

Anatomy (Text-fig. 15)

The pseudobranch contains deep transverse folds, one of which usually covers the anus (Text-fig. 15).

Apart from the presence of 5–6 lobes of the prostate gland instead of 3, the genital organs resemble those described by Lacaze-Duthiers (1899). Wright (1963b) comments that in specimens from Aden the flagellum appears to have a separate opening into the preputium instead of opening into the penis sheath as described by Lacaze-Duthiers. This observation was based on a specimen in which the penis sheath was everted into the preputium ; in other Aden specimens that have been dissected the structure is like that described by Lacaze-Duthiers, as is also the case in Ethiopian specimens.

Radula (Text-figs. 35 and 36)

The central tooth usually bears one small cusp. Median lateral teeth bear a single large cusp, but an ectocone becomes progressively well developed towards the edge of the radula, and is sub-divided into 3 or 4 small cusps on the lateral edge of the marginal teeth. Cusps are absent from the outer marginal teeth. In one longitudinal row of marginal teeth an endocone is present, and in a radula of a specimen from 10 km. N. of Debra Berhan the central tooth bears two small cusps (Text-fig. 35). In certain specimens the cusp on the central tooth is extremely small, and this probably accounts for Jickeli's failure to find this cusp in *A. abyssinicus*. Wright (1963b) illustrates a bicuspid central tooth in *A. fluviatilis* from Aden.

REMARKS. The extent of variation in shell shape in the series (55 specimens) from the River Toquor near Mekerka, suggests that *A. abyssinicus* Jickeli and *A. hamacenicus* Bourguignat, which were originally described from this locality, are synonymous. In view of the probability that the shape of ancylid shells is affected by the substratum on which they grow, the relatively narrow shape of *hamacenicus* may be a modification induced by growth on narrow plant stems. All of the original nine specimens of *hamacenicus* were found on vegetation hanging in the water, whereas *abyssinicus* was collected from stones.

Jickeli observed a close resemblance between small specimens of *A. abyssinicus* and *A. fluviatilis* from Europe, but recognised significant differences between fully grown shells, and in the radulae. Walker (1914) is of the opinion that both Jickeli's species are closely related to *A. fluviatilis*, but Connolly (1941) records *A. abyssinicus* from the Yemen as a distinct species. Wright (1963b) identifies further specimens from Western Aden Protectorate as *A. fluviatilis*, and refers both Connolly's records to this species.

The present collection contains a wide variety of *Ancylus* shells resembling *A. fluviatilis*, and it would be desirable to compare this variation in shell shape with that occurring in Europe, and to assess the significance of differences in conjunction with anatomical information. A detailed study of this kind is beyond the scope of the present work, but it appears that the differences described by Jickeli between *A. abyssinicus* and *A. fluviatilis* are not significant. Of the outstanding shell forms in the present collection, that with a large hooked apex (Text-fig. 43) is similar to the specimen of *A. pileolus* Fer. illustrated by Roth (1856, pl. 2), but the flattened rounded form (Text-fig. 42) does not appear to have been described in Europe.

It is likely that detailed study will reveal differences between *A. fluviatilis* in its European range and the isolated groups of populations in North Africa and the Arabian Peninsula which are probably remnants of a formerly more extensive range.

Two forms described below appear to be distinct from the populations included above in *A. fluviatilis*. It is possible that distinct African forms of *Ancylus* also exist in Algeria (Bourguignat, 1864).

Distribution. *A. fluviatilis* has an extensive range on the central and northern parts of the N.W. massif of the Ethiopian plateau ; the lowest altitude at which specimens were found was 2,240 m. (7,400 ft.). This species reaches the southern limit of its range in N. Africa and the Arabian Peninsula.

Ancylus sp.

Localities. Choa : 30 km. W. of Wolisso (55) ; 89 km. W. of Guder (22) ; 33 km. E. of Bako (62). Kaffa : 28 km. N. of Jimma on Agarro road (35). Sidamo : 15 km. N. of Dilla (27).

Shell (pl. 3, 17 and 18)

The outline is broadly oval with more or less evenly curved sides. The apex is depressed, and situated at about two thirds of the longest dimension from the anterior margin. In 10 shells from 30 km. W. of Wolisso this distance varies between 0·65 and 0·69 of the total length. The blunt apex is not at all hook-shaped apart form the slightly projecting posterior rim of the apical depression. The anterior surface is evenly curved, the posterior surface is more or less straight, except at the apex and near the margin. Radial sculpture is well defined only on the apex, where 60–80 fine ridges extend to near the apical depression. Circular sculpture consists of irregular fine ridges.

Largest shell : L = 7·0 mm. ; W = 5·7 mm. ; H = 2·7 mm. ; ratio H/W = 0·47.

Anatomy (Text-fig. 14)

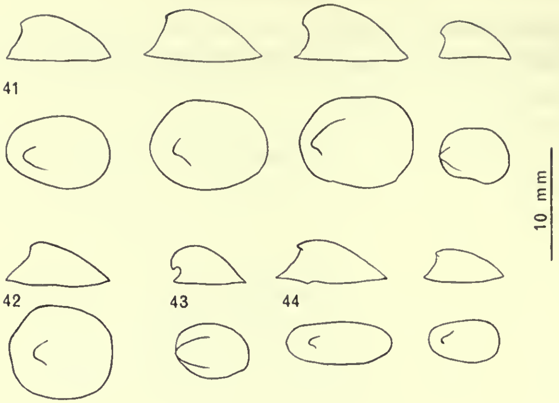
The pseudobranch is a simple lobe, with usually only a trace of the transverse folds that are better developed in *A. fluviatilis*. This appears to be a consistent difference between the two forms, but it must be borne in mind that the appearance of the pseudobranch depends very much on the degree of contraction of the organ. No significant differences have been observed between the genital systems of the two forms.

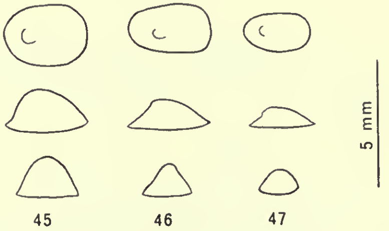
Radula (Text-fig. 38)

There appear to be differences to *A. fluviatilis* in the shape of both the upper and the basal parts of the teeth. The ectocone is relatively well developed on the first lateral tooth, and subdivision of the ectocone begins between the 18th and 20th teeth, instead of at about the 25th tooth in a radula of *A. fluviatilis* of approximately the same shell length.

Remarks. *Ancylus sp.* is characterised by the small maximum individual size, the depressed apex that is not hooked, and the fineness of the radial sculpture. Shells of similar shape are present in one sample of *A. fluviatilis* (Text-fig. 42), but these specimens reach a greater maximum size, and the apical sculpture is relatively coarse. The distribution of *Ancylus sp.* is confined to S.W. Ethiopia, and appears to be isolated from that of *A. fluviatilis*.

Distribution. *Ancylus sp.* has a scattered distribution in S.W. Ethiopia occurring in small stony streams.





Figs. 41–44. Dorsal and lateral shell outlines drawn by camera lucida. Figs. 41–43. *Ancylus fluviatilis*. Fig. 41. River Toquor near Mekerka. Fig. 42. 222 km. S. of Asmara on Addis Ababa road. Fig. 43. 45 km. N. of Gondar on Asmara road. Fig. 44. *Ancylus ashangiensis* sp. n. from Lake Ashangi, paratypes, B.M.N.H.

Figs. 45–47. Dorsal, lateral and posterior outlines. Fig. 45. *Ferrissia isseli* ? from 89 km. W. of Guder. Figs. 46, 47. *Ferrissia clessiniana.?* Fig. 46. 17 km. S. of Adolla. Fig. 47. 46 km. on Carsa road from junction with Dire Dawa-Harar road.

Ancylus ashangiensis sp. n.

Locality. Wollo : E. shore of Lake Ashangi (14).* D. S. Brown, 6.9.62.

Shell (pl. 3, 19 and Text-fig. 44)

The outline of the base is narrow, tapering posteriorly with almost straight sides. The high and sharply pointed apex is slightly turned to the right and situated at about three-quarters of the longest dimension from the anterior margin (in 10 shells this distance varies between 0·72 and 0·86 of the total length). The tip of the shell is produced beyond the apical depression in a lip which is turned upwards so that the apical depression lies horizontally. The anterior surface is slightly convex becoming flattened towards the apex and the anterior margin ; the posterior surface is shallowly concave. Radial sculpture on the apex consists of moderately strong ribs which become less well defined peripherally and do not reach the shell margin. Circular sculpture of fine ridges is present on the apex and there are coarse irregular growth ridges elsewhere.

Holotype (B.M.N.H. coll. No. 1963920) : L = 4·8 mm. ; W = 2·3 mm. ; H = 2·2 mm.

Paratypes, B.M.N.H. and Naturhistoriska Museet, Göteborg. (Gen.-Kat. 1963–11934).

REMARKS. Empty shells were abundant at the waters edge, and at distances of up to several hundred metres from the present shore. The poor development of the peripheral sculpture may in part be due to abrasion of the shells. There is variation in the relative width, but all the shells possess the distinctive sharp apex with a more or less horizontal apical depression, and a relatively narrow basal outline compared to that of *A. fluviatilis*. Of the two species of *Ancylus* previously described from Ethiopia *A. hamacenicus* Bourguignat is the narrower, but is not nearly so laterally compressed as *ashangiensis*. *A. hamacenicus* (= *compressus* Jickeli) was collected together with *A. abyssinicus* by Jickeli who acknowledged (1874, p. 223) that it might be a shell form produced by individuals living on plant stems. Both these species have been discussed above and are regarded as belonging to *A. fluviatilis*. The fact that all the Lake Ashangi specimens have the characteristic narrow shape is against the possibility that this may be merely a response to substratum, and supports the view that the populations are significantly distinct from the other forms of *Ancylus* described in this paper.

Of the *Ancylus* known from other parts of N. Africa, *A. peraudieri* Bgt. and *A. strictus* Morelet (Bourguignat, 1864) resemble *A. ashangiensis* in their basal outline but differ considerably in the shape of the apices.

DISCUSSION

The present collection contains ten forms which are either new or have not been previously recorded from Ethiopia.

Pila speciosa
Physa sp.
Bulinus ugandae
Bulinus sp. (*truncatus* group)
Bulinus sp. (*forskali* group)
Lentorbis junodi
Segmentorbis kanisaensis
Ferrissia isseli?
Ancylus sp. (*fluviatilis* group)
Ancylus ashangiensis

Physa sp., *Ancylus sp.* and *A. ashangiensis* may be regarded as having palaearctic origins ; the seven remaining forms belong to the African fauna.

Ethiopia lies within the North East African Province of the zoogeographical regions of Africa proposed by Pilsbry and Bequaert (1927) on the basis of the molluscan fauna. Bacci (1951) considered that the prevalence of palaearctic forms on the Ethiopian plateaux justified the distinction of an Ethiopian Sub-Province from a Somali Sub-Province. The aquatic gastropod species considered to have palaearctic relationships by Bacci are listed below together with those in the present collection :

Bacci (1951)	Present Collection
Theodoxus africanus	—
Valvata nilotica scioana	*Valvata sp.*
—	*Physa sp.*
Radix pereger	—
Galba truncatula	*Lymnaea truncatula*
Ancylus abyssinicus	
A. hamacenicus	*Ancylus fluviatilis*
—	*Ancylus sp.*

The following species are known only as empty or sub-fossil shells.

—	*Ancylus ashangiensis*
Hydrobia gortanii	—
Tropidiscus planorbis parenzani	*Planorbis planorbis parenzani*

Zoogeographical significance cannot be attached to the present record of a single population of *Physa* as a similar species occurs, probably as a result of introduction by human agency, further south in Africa. Significant additions to Bacci's list of palaearctic forms have thus been made only in the genus *Ancylus*. On the other hand, of the additional forms belonging to the African component in the fauna, four were found on the plateau : *L. junodi*, *S. kanisaensis*, *Bulinus sp.* (*forskali* group) and *Ferrissia isseli?* and three : *Pila speciosa*, *Bulinus ugandae* and *Bulinus sp.* (*truncatus* group) at lower altitudes. *Burnupia caffra* is another species of African affinities that occurs on the plateau and was not known to Bacci.

The present collection increases the number of forms of freshwater gastropod molluscs of African rather than palaearctic affinities known to occur in Ethiopia, but it may be concluded from the wide distribution of *L. truncatula* and the genera *Valvata* and *Ancylus*, together with the diversity of forms within the *Ancylus fluviatilis* species group, that these are long established representatives of the palaearctic fauna on the Ethiopian plateaux.

SUMMARY

A collection of freshwater Gastropoda comprising 28 forms, 10 of which have not been previously recorded from Ethiopia, is described.

Ancylus ashangiensis sp.n. belonging to the *Ancylus fluviatilis* species group is described.

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ABBREVIATIONS USED IN FIGURES AND TEXT

an	anus
ag	albumen gland
agl	cut edge of duct within albumen gland
bp	brood pouch
br	branchial ridge
cm	columellar muscle
ct	ctenidium
dl	dorsal lamella
fp	fertilisation pocket
H	shell height
hd	hermaphrodite duct
L	shell length
lm	left anterior shell adductor muscle
lt	left tentacle
ML	aperture length
mp	mantle process
mct	cut edge of mantle
med	median rectal ridge
ov 1–3	oviducts 1–3
p	penis
pa	papilla
pg	preputial gland
pm	posterior shell adductor muscle
pn	pulmonary siphon
PP	preputium length
pr	prostate
PS	penis sheath length
r	rectum
rm	retractor muscle
rr	lateral rectal ridge
sv	seminal vesicle
t	testis
UD	umbilicus diameter
ur	ureter
ut	uterus
va	vagina
vd	vas deferens
vl	ventral lamella
W	shell width
♂	male aperture

LOCALITIES REFERRED TO IN TEXT

References are to the East African Metre Grid 1 : 500,000 G.S.G.S. 4355, and for Harar only G.S.G.S. 1401 (First Edition, 1960). It should be noted that the spelling of place names is variable, and that many old town names are being replaced by modern Amharic names.

Adamitullo	HCT 3269
Adi Ugri	HFL 4147
Adolla	HCE 6650
Adowa	HFE 5166
Agarro	HCR 0568
Akaki	HDE 4280
Ambo	HDD 3992
Argereselam	HCL 1219
Asmara	HFL 6496
Assendabo	HCR 6656
Bahar Dar	HEC 9182
Batei	HEF 7037
Bishoftu (Debra Zeit)	
Bonga	HCP 6002
Carsa	DJ 3045
Cheren	HFT 0243
Debra Berhan	HDM 2269
Debra Markos	HDS 2442
Debra Zeit	HDE 6267
Decamere	HFL 6669
Dessie	HEF 3331
Dilla	HCK 9008
Dire Dawa	DJ 3160
Dollo	JBJ 5362
Dukem	HDE 5472
Filtu	JBN 9666
Ghion (Wolisso)	HDD 5344
Gondar	HEJ 9894
Gorgora	HEJ 8154
Goro Gomoto	HDE 5030 approx.
Guder	HDD 3191
Harar	DJ 6028
Hagere Hiwot (Ambo)	
Jimma	HCR 2748
Kombolchia	HEF 4425
Kombi	HDD 0804
Koka	HDE 8237
Lake Abaya (L. Margherita)	
Lake Abyata	HCT 2741
Lake Aramyia	DJ 4539
Lake Ashangi	HEM 2190
Lake Awasa	HCL 1882
Lake Biete Mengest	HDE 6469
Lake Bishoftu	HDE 6269
Lake Guder (Lake Hora)	
Lake Haik	HEF 3852
Lake Hora Harsadi, or Orsedi (Lake Beite Mengest)	

Lake Hora	HDE 6471
Lake Margherita	HCK 6607
Lake Shala	HCT 2525
Lake Wonji	HDD 4773
Lake Zwai	HCT 4169
Lekemti	HDH 9505
Massawa	HFU 1018
Medhanie Alem	HFD 6802
Mekerka	HFT 3910
Moggio (Mojo)	HDE 7851
Nazareth	HDE 9445
Neghelli	HBU 3910
Nego	HDE 7530 approx
River Awash (S. of Nazareth)	HDF 0229
River Ganale Doria	JBJ 3384
River Toquor (at Mekerka)	
Saati	HFT 8825
Shashamanne	HCL 2198
Soddu	HCK 2857
Sokuru	HCR 9173
Teramni	HFL 4260
Uachile Wells	HBT 7202
Wolisso	HDD 5344
Wondo	HCL 0130

PLATE 1

FIG. 1. *Bellamya unicolor* from Lake Tana, large specimen. (× 1·5).

FIG. 2. *Bellamya unicolor* from Lake Tana, small specimen. (× 3).

FIG. 3. *Bellamya unicolor* from 5 km. S. of Adamitullo, sub-fossil. (× 3).

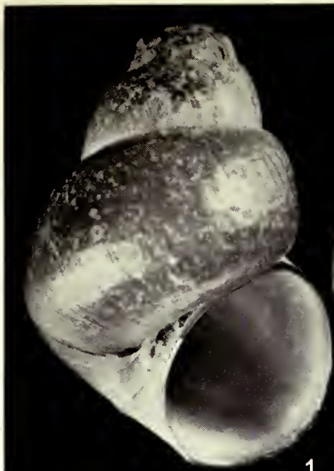
FIGS. 4, 5. *Valvata* sp. from 1 km. S. of Debra Berhan. (× 7·5).

FIGS. 6, 8. *Valvata* sp. from 72 km. N. of Addis Ababa on Debra Markos road. (× 7·5).

FIGS. 7, 9. *Valvata* sp. from Lake Wonji. (× 7·5).

FIG. 10. *Lymnaea natalensis.* 38 km. N. of Jimma on Agarro road. (× 3).

FIG. 11. *Lymnaea natalensis* from Lake Tana at Gorgora. (× 3).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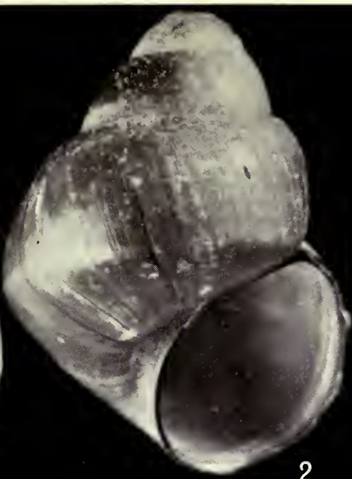
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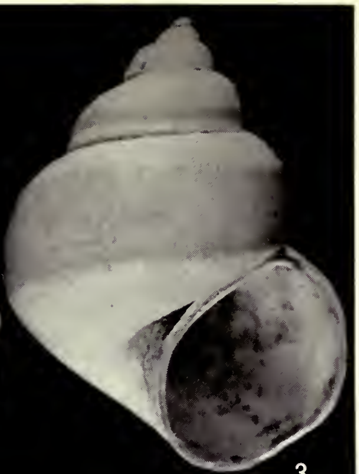
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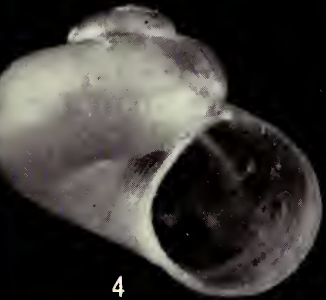
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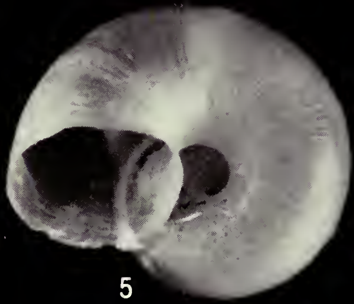
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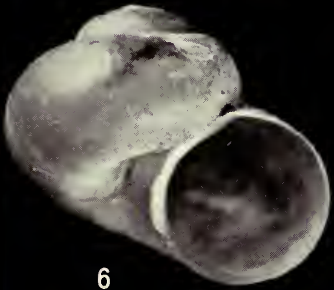
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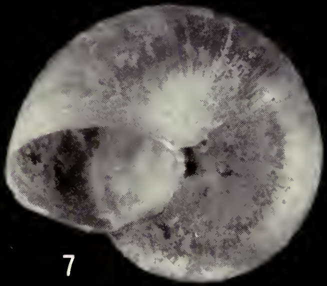
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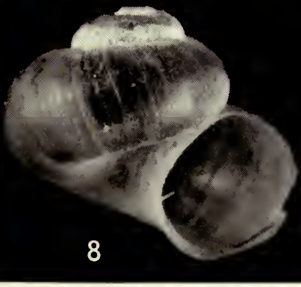
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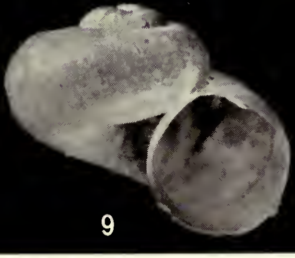
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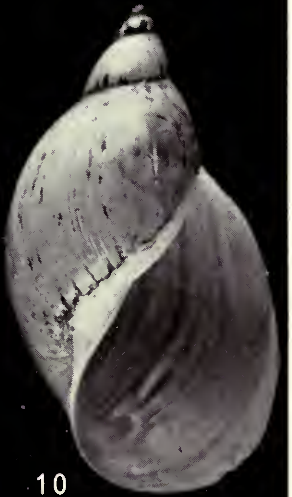
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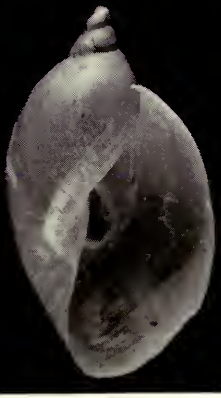
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PLATE 2

Fig. 1. *Physa* sp. from outflow below Koka Dam.

Fig. 2. *Bulinus truncatus sericinus* from 38 km. N. of Gondar.

Fig. 3. *Bulinus truncatus sericinus* from Lake Hora.

Fig. 4. *Bulinus* sp. from Lake Awasa.

Fig. 5. *Lymnaea truncatula* from 19 km. N. of Gondar.

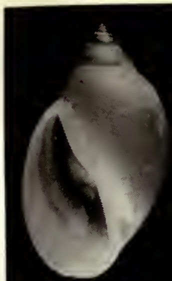
Figs. 6, 7, 10. *Bulinus ugandae* from Lake Margherita.

Figs. 8, 11. *Bulinus africanus ovoideus* from Lake Tana.

Figs. 9, 12. *Bulinus africanus ovoideus* from 14 km. N. of Medhanie Alem.

Figs. 13–15. *Bulinus africanus ovoideus* from 5 km. W. of Assendabo.

All figures are × 3.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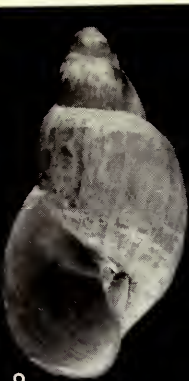
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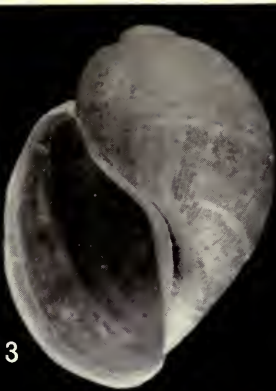
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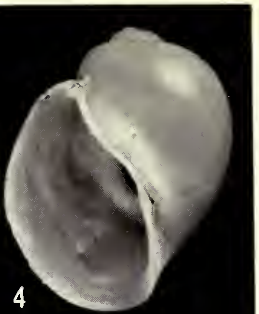
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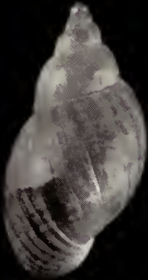
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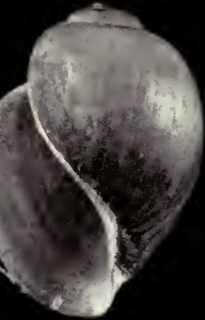
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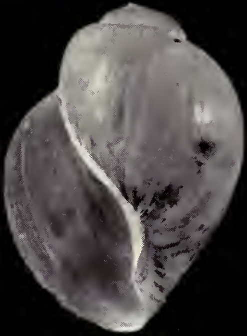
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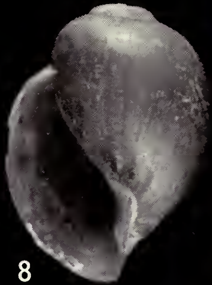
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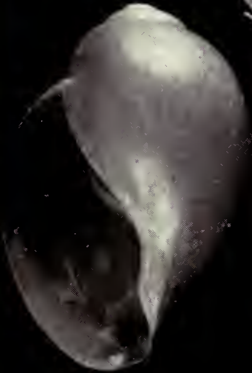
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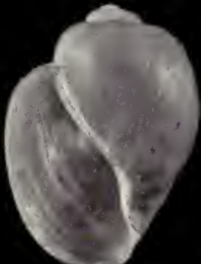
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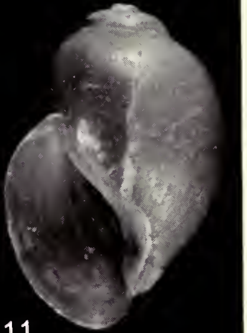
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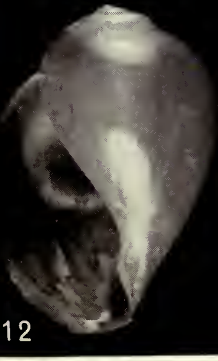
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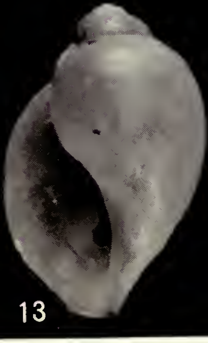
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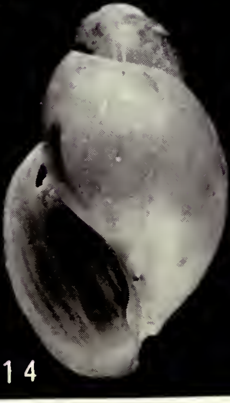
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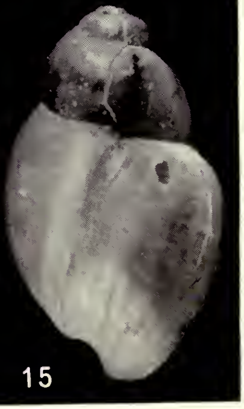
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PLATE 3

FIG. 1. *Bulinus forskali* from Lake Tana.

FIG. 2. *Bulinus forskali* from Lake Margherita.

FIG. 3. *Bulinus scalaris* from 4 km. N. of Gondar.

FIG. 4. *Bulinus* sp. from 4 km. N. of Medhanie Alem.

FIGS. 5, 6. *Gyraulus costulatus* from 0·5 km. S. of Adowa on Gondar road. (× 7·5).

FIGS. 7–9. *Biomphalaria sudanica* from Lake Zwai.

FIGS. 10, 11. *Gyraulus costulatus* from 9 km. N. of Dessie. (× 7·5).

FIGS. 12–14. *Biomphalaria sudanica* from Lake Abyata.

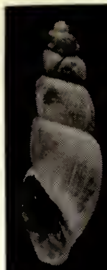
FIGS 15, 16. *Planorbis planorbis parenzani* from 5 km. S. of Adamitullo, sub-fossil. (× 7·5).

FIG. 17. *Ancylus* sp. from 28 km. N. of Jimma on Agarro road, lateral, posterior and dorsal views.

FIG. 18. *Ancylus* sp. from 15 km. N. of Dilla, lateral, posterior and dorsal views.

FIG. 19. *Ancylus ashangiensis* sp.n. from Lake Ashangi, lateral, posterior and dorsal views. Holotype B.M.N.H. coll. no. 1963 920.

All figures are × 3 unless otherwise stated.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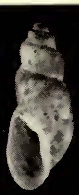
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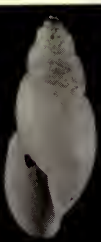
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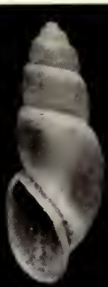
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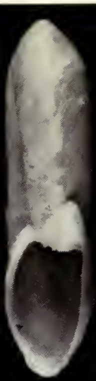
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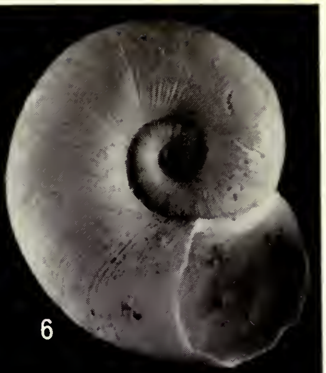
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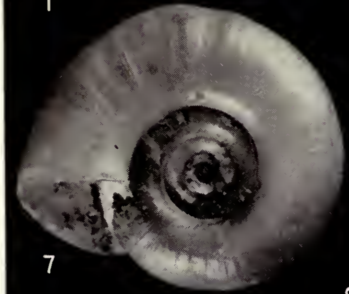
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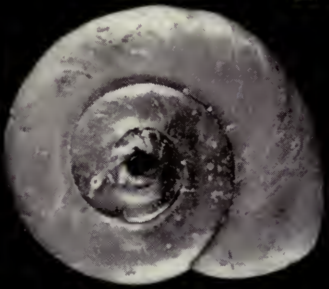
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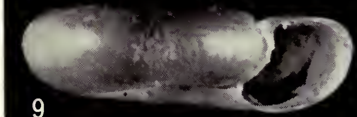
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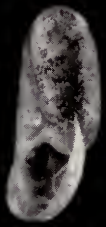
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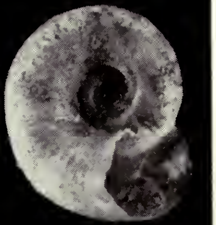
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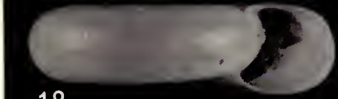
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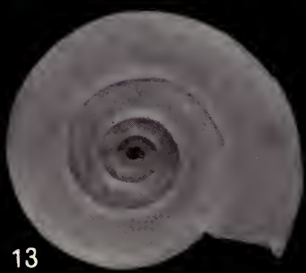
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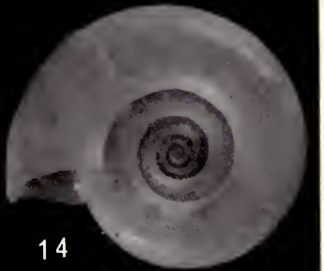
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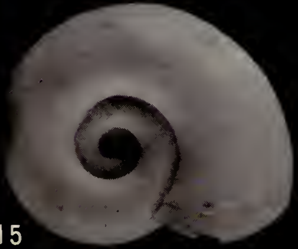
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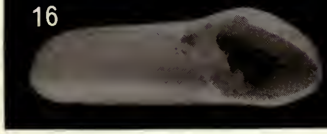
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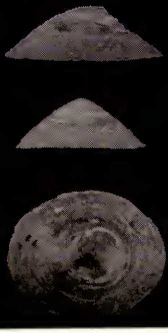

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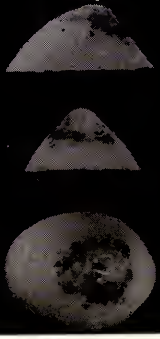

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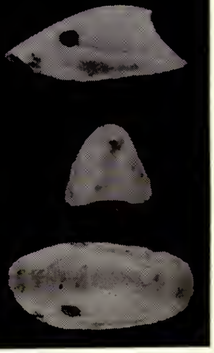

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THE BRITISH MUSEUM (NATURAL HISTORY) EXPEDITION TO EAST NEPAL 1961-62

INTRODUCTION AND LISTS OF LOCALITIES

BRITISH MUSEUM 2 APR 1965 NATURAL HISTORY

J. G. SHEALS AND WILLIAM G. INGLIS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 12 No. 3
LONDON : 1965

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Pp. 95 – 114 ; 7 *Plates* ; 1 *map*

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THE BRITISH MUSEUM (NATURAL HISTORY) EXPEDITION TO EAST NEPAL 1961-62

INTRODUCTION AND LISTS OF LOCALITIES

By J. G. SHEALS & WILLIAM G. INGLIS

INTRODUCTION

As a complex transitional zone the Himalayan region is of outstanding biogeographical interest. Extending for 1,500 miles from Upper Burma in the East to Afghanistan in the West, this system of Tertiary mountains forms an almost unbroken chain between the Indo-Gangetic Plain and the high plateaux of Central Asia. Zoogeographically the elevation is responsible for a remarkable southerly extension of the Palaearctic zone resulting in a peculiar confluence of Indian, Indo-Malayan, Mediterranean and Northern Palaearctic elements, while floristically the range forms a unique corridor between tropical India and arid Central Asia enabling plants of the temperate Sino-Japanese region to migrate westwards to the border of the African-Indian desert.

A detailed geographical account is given by Burrard & Hayden (1907). The system is not a single mountain chain but a complex series of nearly parallel ranges separated by valleys and high plateaux. Three longitudinal groups can be readily recognised. The Great Himalaya, an inner range on which lie the highest peaks; the Lesser Himalaya, a series of ranges rising to approximately 15,000 ft. and an outer system of foothills, the Siwaliks, contiguous to the Tarai forest and the plains of India. Although their upheaval was probably accompanied by a further elevation of the inner ranges, the Siwaliks are more recently formed and, in many places, a unique system of longitudinal valleys or Duns is found between these foothills and the intermediate ranges. The Himalayas can also be conveniently divided into four East-West sections and of these the least known yet possibly the most interesting biologically is the Central or Nepal Himalaya. This section, approximately 500 miles in length lies almost entirely within the present political boundaries of Nepal but geographically is defined as that portion of the system lying between the Tista and Kali rivers. The major peaks include Kanchenjunga, Everest, Makalu and Dhaulagiri and the general trend of the Great range in this section is from East to North of West except near the eastern extremity where the long Singalila ridge extends abruptly Southwards to the plains from the Kanchenjunga massif. Each section of the Himalayas has certain characteristic features. In Nepal the dun valleys are well marked and there is a tendency for the great peaks to stand in clusters or rows, each aggregation being known to the Nepalese as a Himal, e.g. Langtang Himal and Jal Jale Himal. The five principal rivers of the Nepal Himalaya are the Karnali, Rapti, Bagmati, Gandak and the Kosi, all affluents of the Ganges. The Karnali and Rapti systems drain the western area between the Garhwal border and Dhaulagiri, and the great basin of the Gandak occupies the central zone between the Annapurna and Langtang Himals. The Bagmati rises in the lesser ranges and drains the Central Nepal Valley, while the Kosi, one of the most important of all the Himalayan rivers, drains the region east of Gosainthan. Its principal tributary, the Arun, cuts an impressive gorge through the Great Range a few miles East of Mount Everest, and its most easterly affluent, the Tamur, drains the South-western face of Kanchenjunga and the Western slopes of the Singalila ridge.

PREVIOUS BIOLOGICAL EXPLORATION

The isolationist policy adopted by Nepal until 1947 was so rigidly enforced that Landon (1928) was able to present a list of all the Europeans who had visited the country during the period 1881–1925. During these 45 years about 153 persons visited Nepal for military, official and antiquarian purposes and 55 as guests of the Maharaja. Although there was no general prohibition against Asiatics, with one notable exception even the most privileged Europeans were forbidden to travel outside the Tarai or, in upland Nepal, more than a few miles beyond the narrow limits of the Kathmandu Valley. Despite these restrictions, however, significant biological contributions were made during the 19th century.

The early botanical work, culminating in the publication of Don's *Prodromus Florae Nepalensis* (1825) and Wallich's *Tentamen Florae Napalensis* (1824–26), began with the visit of Francis Buchanan (later Hamilton), botanist and physician, to Kathmandu in March 1803. Buchanan stayed in the Valley for about a year and later (1807–1814) directed a great botanical survey of north and west Bengal, detaching Asiatic members of his staff to collect economic plants from the Nepal Himalaya (Prain, 1905, Burkill, 1953). Shortly after the appointment in 1816 of Edward Gardner as first political Resident at Kathmandu, Nathanial Wallich, then in charge of the East India Company's Botanic Garden at Calcutta, sent two collectors to work under the Resident's direction. They appear to be those who sent the first seed of *Rhododendron arboreum* to England in 1818 (Burkill op. cit.). Wallich himself spent the year 1821 in Kathmandu but like Buchanan was hampered by restrictions on his movements although his collectors penetrated deep into the mountains along the pilgrims' road to Gosainkund. David Don, who curated the private collections of Aylmer Bourke Lambert, based his *Prodromus* on Buchanan's Kathmandu material, part of this collection having been presented to Lambert in 1806, but he also studied Nepalese plants sent to Lambert by Wallich. A substantial part of Lambert's herbarium, including the Buchanan collection, was purchased by the British Museum in 1842.

A number of mosses collected by Gardner, Buchanan and Wallich are described in W. J. Hooker's *Musci Exotici* (1818, 1820). Gardner & Wallich also presented a number of birds, mammals and many insects from Nepal to Major General Thomas Hardwick. Some of these Hardwick described, others he presented to the British Museum and to the Zoological and Linnean Societies. Hardwick returned to England in 1823 and assisted Gray (1830–35) with the first volumes of the projected *Illustrations of the Indian Fauna* (Kinnear 1925, Sawyer 1953).

Brian Houghton Hodgson was Assistant Resident, and later Resident, at Kathmandu during the period 1820–1843. Diplomat, oriental scholar and antiquarian, he has been described as one of the greatest and least thanked of all our British Residents and one of the greatest labourers in the sphere of Indian research and record (Hunter 1896, Landon 1928). His contributions to zoology were no less distinguished. He early appreciated the zoogeographical significance of the Himalayas and recognised a faunal zonation associated with altitudinal differences. During his service at Kathmandu he laid down the foundations of Himalayan mammalogy in upwards of 70 scientific papers. His interests also extended to ornithology and it is probably in this field that his greatest zoological contributions were made. After leaving Kathmandu he continued his researches in retirement at Darjeeling, returning to England in 1858. The most important part of his collections of specimens and drawings was presented to the British Museum (Gray 1863) and the smaller part originally presented to the East India Company's Museum was merged with the main collection in 1881. Hodgson's many zoological papers are catalogued by Hunter (1896) and amongst the early reports on his fish and reptile collections are those of Cantor (1839) and Gunther (1860, 1861, 1864).

Sir Joseph Hooker's remarkable exploration of East Nepal is described in his famous *Himalayan Journals* first published in 1854. It is surprising that this visit to Nepal was sanctioned but some light is thrown on the circumstances by Hooker's recollections in Hunter's *Life* " I owe it entirely to his (Hodgson's) personal influence with the late Sir Jang Bahadur that I was permitted to travel in Eastern Nepal over ground never before or since traversed by any European and to visit the jealously guarded passes of the Nepalese Tibet frontier ". Hooker left Hodgson's house at Darjeeling on 27th October 1848 and with a party of 56, including a guard of 6 Nepalese soldiers and 2 officers and " Mr. Hodgson's bird and animal shooter, collector and stuffer ", crossed the Singalila ridge near Tanglu on 5th November : Hooker's route in Nepal can be fairly easily traced, although problems of transliteration render the identity of a few localities problematical. Crossing the " Sakkiazung ridge " (Mahabharata Lekh) near Malinge he descended to the Hima Khola which he followed to its junction with the Tamur. He then made his way up the valley to Walungchung Gola passing through " Mywa Guola ", which, from his description must certainly be the trading village now called Dobhan (sometimes spelt Dumuhan). After exploring the region of the " Wallanchoon Pass " i.e. Tiptala Bhanjyang (16,740 ft.) he followed the Yangma Khola to Yangma Village and thence to the Tibetan frontier again at Khangla Deorali (18,315 ft.). Traversing the high ridge South of Yangma he then explored the Ghunsa Khola as far as " Kambachen " (Khamachin). On 5th December he began his southward trek, and crossing the Simbua Khola near Chairam, passed through " Tchonboong " (? Phungphung) and Sablakhu. Finally he followed the upper reaches of the Kabeli and on 15th December recrossed the Singalila a few miles North of Phalut. After exploring Sikkim and Assam, Hooker returned to Britain in 1851 and in conjunction with Thomas Thompson produced the first volume of the projected *Flora Indica* (1855) but the series was subsequently abandoned owing to lack of financial support. Much of Hooker's bryophyte material is described by Mitten (1859, 1860).

During the remainder of the 19th century almost the only contributions were those made by the members of the Residency Staff, although a collector of the Indian Museum appears to have visited Kathmandu in 1871. In the preface to his *Lepidoptera Indica* Moore (1890) acknowledges the collection of numerous specimens of moths from Nepal made by Major General G. Ramsay, Resident during the period 1852–67, while the Residency Surgeon from 1876–1878, John Scully, published on birds (1879) and later on the Chiroptera (1887). During the latter part of the 19th century several major compilations on the flora and fauna of the Indian sub-continent appeared (e.g. Hooker's *Flora of British India*, 1872–1897 and the first monographs of the *Fauna of British India*) but in relation to the Nepalese species these were substantially dependent on the collections made before 1850.

Boulenger, Annandale, Wall & Regan (1907) reported on a collection of fish, amphibia and reptiles made in the vicinity of Kathmandu in 1906 by R. Hodgart, a collector of the Indian Museum, while I. H. Burkill, a botanist, also of the Indian Museum, visited Kathmandu at the end of 1907. In his notes on the journey Burkill (1910) includes a list of plants and gives an account of the cultivation and zonation of vegetation in the Valley and on the route between Raxaul and Kathmandu.

In 1912 the Bombay Natural History Society initiated the Mammal Survey of India with the primary object of obtaining topotypes for systematic studies and to investigate the variation and distribution of the fauna in the sub-continent. Collections in Nepal were made during August 1920–March 1921 by the British Envoy, Lt. Col. R. L. Kennion, with the assistance of the Society's collector N. A. Baptista. The localities covered were the Tarai, the Duns (Rapti Valley), the Kathmandu Valley and the basin of the Gandak up to 50 miles North of Kathmandu. A scientific report on this collection was made by Hinton & Fry (1923). A further collection in the districts west of Kathmandu was made by Baptista during the year May 1922–May 1923 and a supplementary report was written by Fry (1925). Collections of birds made during this time by Kennion and Baptista were of value in confirming the status and distribution of a large number of species (Prater 1928).

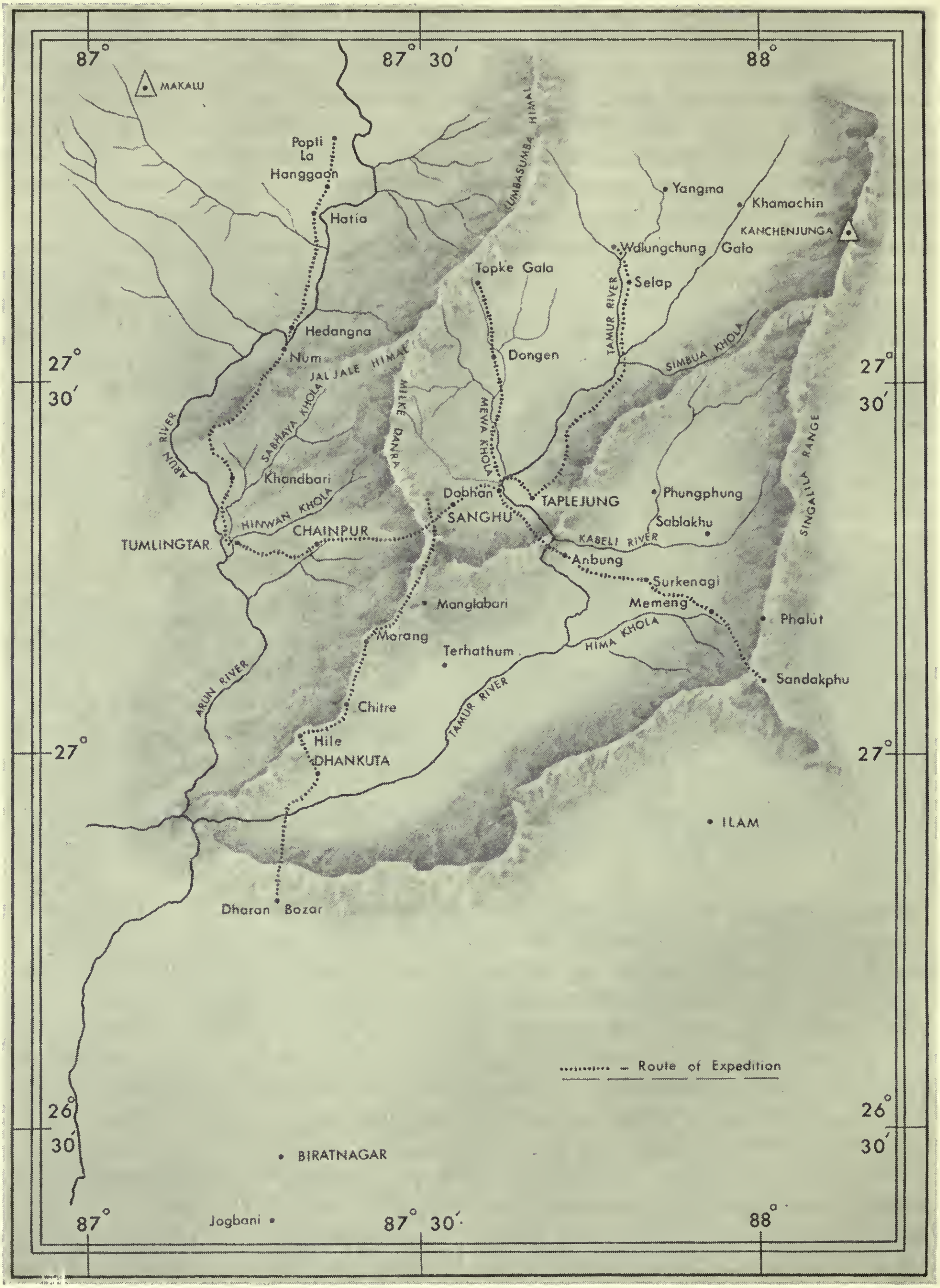
Hay (1934) observes that the serious botanical exploration of Nepal did not commence until 1928 when the Prime Minister, Maharaja Chandra Sham Sher, appointed Major Lall Dhwoj to collect seeds and specimens. Dhwoj collaborated with the Forest Research Station, Dehra Dun, in a brief exploration of S.W. Nepal in the Spring of 1929 (Parker 1932) and subsequently collected in Central and East Nepal. Many hundred sheets of specimens were received by the British Museum (Natural History) and to him is credited the introduction of several fine plants including *Gentiana ornata*. Dhwoj died in 1931 and was succeeded by Professor K. Sharma who made extensive and valuable collections during the period 1931–1937. Valuable plant collections were also received at this time from Lt. Col. F. M. Bailey, Envoy at Kathmandu during the period 1935–38. An eminent Lepidopterist, Bailey made collections in the Tarai and in the Valley, while the Nepalese workers whom he trained brought in botanical and zoological material from West Nepal and from the country North of Kathmandu (Bailey 1951).

Zoological exploration after the second world war appears to have been initiated by S. Dillon Ripley, an ornithologist who visited the Valley in April and May 1947. Later that year another ornithologist, B. E. Smythies, received permission to make a fortnight's tour of the pilgrim trail to Gosainkund with the stipulation that he did not go within 5-6 miles of the Sacred lakes (Smythies 1948). This almost unprecedented concession foreshadowed a more liberal attitude by the Nepalese Authorities and, apart from certain minor restrictions, after the beginning of 1948 the barriers to foreign exploration were gradually removed. As a result, since 1949 a large number of expeditions have visited Nepal. The majority of these have been primarily mountaineering, although many have had secondary biological objectives, for example Tilman's expedition to the Langtang and Annapurna Himals (Tilman, 1952) and the Californian Himalayan Expedition to Makalu (Houston & Long, 1955 ; Leviton, Myers & Swan, 1956). The British Museum (Natural History) and Royal Horticultural Society jointly sponsored expeditions to West Nepal in 1952 and 1954 (Williams, 1953 ; Sykes, 1956). These expeditions were mainly concerned with flowering plants although both made small but valuable entomological and other zoological collections. Additionally, biological studies in the Nepal Valley have been continued by Mrs. D. Proud (1949, 1952, 1955) and by Herklots (1962).

THE 1961-62 EXPEDITION

The project was planned with a view to obtaining botanical, entomological and other zoological material from the Eastern part of the Nepal Himalaya, a comparatively little-known area but potentially interesting by virtue of its position along the confluence of distinctive biogeographical zones. The greater part of the work was carried out in the Dhankuta province between the Arun River in the West and the Kanchenjunga Massif and the associated Singalila Range in the East. The botanical programme was directed mainly towards the Cryptogamic flora, particularly the Bryophyta, while the primary concern of the zoologists was an investigation of the Micro-arthropoda and Nematoda of soil, forest litter and allied habitats.

As the collection of phanerogamous plants was not a major objective the choice of season for the field work was less restricted. Although greater populations of insects might be expected during the main flowering season from April to August a great part of this season coincides with the monsoon period when travel in the hills is difficult and hazardous owing to swollen torrents. Moreover, during these months the high humidities might severely limit the efficiency of the desiccation funnels used for collecting micro-arthropoda. Consequently the field work was planned to begin at the end of the monsoon and the collections were actually made between 17th September 1961 and 20th March 1962. However, there was still a certain conflict of requirements. The botanist, and to a certain extent the entomologist, sought a wide cover of the area under investigation and their collecting techniques did not preclude continuous movement, but the zoologists required a permanent shelter to house their bulky apparatus. Also the zoologists' interests were centred largely around the forests of Rhododendron and Evergreen Oaks at altitudes where


87°
87° 30′
88°
MAKALU
Popti La
Hanggaon
Hatia
LUMBASUMBA HIMAL
Yangma
Khamachin
KANCHENJUNGA
Walungchung
Gola
Topke Gola
Selap
TAMUR RIVER
Hedangna
Num
Dongen
SIMBUA KHOLA
27° 30′
JAL JALE HIMAL
SABHAYA KHOLA
MILKE DANRA
MEWA KHOLA
ARUN RIVER
Khandbari
Dobhan
TAPLEJUNG
Phungphung
HINWAN KHOLA
SANGHU
Sablakhu
SINGALILA RANGE
CHAINPUR
TUMLINGTAR
KABELI RIVER
Anbung
Surkenagi
Memeng
Manglabari
Phalut
Morang
HIMA KHOLA
Terhathum
Sandakphu
ARUN RIVER
TAMUR RIVER
Chitre
Hile
DHANKUTA
27°
ILAM
Dharan Bazar
Route of Expedition
26° 30′
BIRATNAGAR
Jogbani

Sketch map of East Nepal : scale 16 miles to the inch (approx.).

the population of winged insects would almost certainly be low after mid November. To meet these varied requirements it was planned to acquire some type of building at an altitude of about 5,000 ft. in the Taplejung region, and to use this as the nucleus of a base camp from which excursions could be made to all parts of the Eastern region.

There are two practical routes from India to the Taplejung area. The eastern route leads from Darjeeling over the Singalila at Sandakphu or Phalut and thence by way of Memeng and Anbung to the middle reaches of the Tamur. The southern approach is from Jogbani, Bihar State, via Dharan Bazar and Dhankuta. For a small party with a moderate amount of equipment the Darjeeling route is certainly preferable, for mechanical transport can be used as far as the crest of the Singalila and from this point the 5–6-day march is not severe, but for a large party with bulky stores the road and rail transport problems are less complicated on the southern route. Early in the planning stage the Commanding Officer of the H.Q. British Gurkha Lines of Communication at Dharan offered his full co-operation and it was resolved to use Dharan as an initial base where porters could be recruited and the bulked stores split into man-loads.

The stores and equipment, weighing approximately 3½ tons, were taken by sea to Bombay and thence by rail, via Calcutta, to Jogbani and the final 30 mile road trip to Dharan was made in trucks belonging to the Brigade of Gurkhas. The Expedition left Dharan for the hills with 119 porters on 17th September 1961.

The success of the plan hinged largely on securing the use of a permanent building and a small reconnaissance party was fortunate in finding a suitable rest house or Dharam Sala at Sanghu, a small village at an altitude of about 6,000 ft. on the slopes of the Maewa Khola Valley. The village elders were co-operative and an added attraction was a level grass plot immediately in front of the Dharam Sala which would accommodate a large base camp. Sanghu was very near the geographical centre of the Dhankuta province and although the land in the immediate vicinity of the village was intensely cultivated, extensive forests of Evergreen Oak and Rhododendron could be reached within about two to four hours. The main party arrived at Sanghu on 26th September and the porters were paid off the following morning.

The ground floor of the Dharam Sala was equipped as a kitchen and the first floor as a laboratory-cum-messroom ; tables, shelves, and racks for the soil extraction apparatus being cheaply made in bamboo. The attic space provided additional storage for canned foods and equipment. Water supplies at Sanghu were always adequate but initially some difficulty was experienced in securing food supplies for the permanent staff of field assistants. This problem was solved by the energetic efforts of the Sirdar and after the October harvest supplies were always adequate. Kerosene for lighting and cooking was always available but rather expensive at about 8/– per gallon. Communication with Dharan, mainly for the purpose of sending and receiving mail, was maintained by runner. During the whole time of the Expedition Sanghu base was manned by some British members of the Expedition except during the period 4th–31st December, and during the last 2 weeks of January when subsidiary bases for the exploration of the Arun and Tamur Valleys were set up at Tumlingtar and Dobhan respectively. Health problems were few, blood-sucking insects did not constitute a problem even at low altitudes but leeches were troublesome until the end of the monsoon and were common up to altitudes of 12,000 ft. It was found that leeches detached themselves immediately when given a short spray with a piperonyl butoxide/pyrethrum aerosol preparation.

Sanghu (27° 21′ N, 87° 33′ E) is at about 6,000 ft. on the south side of one of the terminal branches of the Maewa Khola near the Western end of the main valley system. The river runs West to East and rises on the slopes of a North-South-running ridge, the Milke Danra, which is about 11–12,000 ft. high in this area. The valley is steep-sided and narrow so that the village is somewhat enclosed by high ground particularly to the South and West. Sanghu, not marked on some maps, lies east of Tamrang and west of Tembe. It is not a compact group of houses and the name applies to the south side of the valley between two major streams. The Dharam Sala, which was used by the Expedition, and the school building lie on one of the very few flat areas of ground, just beside the main East-West track running from Taplejung in the East to Chainpur in the West crossing the ridge by a pass—the Milke Bhanjyang—at about 11,000 ft. The entire valley side is carved into small paddy fields, up to about 7,500 ft., and is very densely cultivated. On the high ridges behind the camp is a belt of Evergreen Oak forest from 7,500 ft.–9,300 ft. and above this, Rhododendron forest extends about to the top of the ridge which is bare of large bushes or trees. The area produces large quantities of oranges (Santala), which—with bananas—grow up to about 6,000 ft. The main food crop is rice, with some potatoes and other vegetables of minor importance. Domestic animals are cattle, water-buffalo, sheep, pigs and hens. Because of the intensity of the farming the only uncultivated land below 7,500 ft. tended to be in the gullies and on very steep slopes, although the walls of the paddy fields afforded a minor habitat of some interest.

The river to the west of Sanghu (between Sanghu and Tamrang) passes, at one point, through a narrow gorge bounded by steep cliffs about 200 ft. high. The flat area of sandy soil at the bottom of the gorge, bordered on the west by the river and the east by a steep bank covered by mixed vegetation, afforded an isolated natural area unaffected by cultivation.

Dobhan (27° 22′ N, 87° 37′ E) lies at the junction of the Maewa Khola and Tamur River about half-a-day's march East of Sanghu at an altitude of about 2,500 ft. It is a major trading centre with a number of permanent shops. There is a small, flat plateau lying North–South in the junction of the two rivers both of which are crossed by chain bridges. The soil is very light and sandy with a certain amount of mica.

Tumlingtar (27° 18′ N, 87° 13′ E) is an extensive flat plateau lying at about 1,800 ft. between the Arun River and the Sabhaya Khola at their junction. The plateau is bounded by steep cliffs, about 150–200 ft. high and is extremely dry with only very few pools of stagnant water so that most water for use on it must be carried up from the rivers. The soil on the plateau and the surrounding areas is poor, sandy, and red in colour with a high mica content. The edges of the plateau and the steep hills bordering the valley systems are marked by deep and extensive erosion gullies. The cliffs on the west side, bordering the Arun River are very steep while those on the east are less vertical with a fairly extensive flood plain between their bottom and the Sabhaya Khola. As at Sanghu and Dobhan every available piece of land is cultivated. The most obvious feature of the entire area was this extensive cultivation. Virtually every scrap of land which could be used for crops was used with a great reduction and, in some localities, elimination of any natural habitat.

BOTANY

Over 5,000 botanical specimens were collected. Special attention was paid to bryophytes and lichens and together these constituted over 75% of the material collected. About 300 phanerogams and a similar number of pteridophytes were also dried. The conditions in the main areas investigated were much more moist than had been expected and the profusion of bryophytes generally was extremely gratifying. In particular the rich hepatic flora in the immediate vicinity of Sanghu base provided scope for intensive study. The rocks and shaded stream banks in gullies bore a profusion of bryophytes and bamboo thickets in these gullies harboured many unusual mosses of the family Sematophyllaceae. Small bryophyte species were plentiful on north-facing walls of rice terraces and were also abundant on the trunks of trees and on moist ground in the Evergreen Oak forests at about 7,500–9,000ft. Above this altitude, in the Rhododendron forests, foliaceous lichens, particularly *Anaptychia* and *Usnea* species, were common. The dry Tumlingtar plateau, which was visited in December, provided a sharp contrast with the Sanghu area. Here hepatics were uncommon but in shaded habitats mosses were plentiful although limited to a few species. The steep cliffs above the Sabhaya and Arun Kholas supported a remarkable flora of crustaceous lichens. On the open cliffs there were also patches of xerophytic *Selaginella* and in the less exposed areas colonies of *Fissidens* species were not uncommon.

A camp was made for a few days in the Mewa Khola gorge above Dongen. In this remote and unspoiled area the dense forests (predominantly oak) were extremely rich localities and would have provided scope for several weeks' collecting. Unfortunately inclement weather made a longer stay impossible. Of particular interest was the profuse flora of smaller mosses and hepatics carried by the branches of shrubs. Amongst the hepatics the smaller Lejeuniaceae were prominent on the bare parts of twigs and stems and also on fern fronds. *Daltonia* species were also common and this was the only locality where species of *Distichophyllum* were found.

In February a short visit was paid to the Tarai forest immediately south of Dharan. A few mosses were collected but at this time conditions were much drier than in the hill forests and Cryptogams were not abundant.

LOCALITIES

SANGHU BASE CAMP AREA. 27° 21′ N., 87° 33′ E. Alt. 5,500–7,000 ft. 2.x.61–4.xii.61, 1.i.62–16.i.62, 11.ii.62–19.ii.62.

Numerous habitats in immediate vicinity of camp site, including walls, rocks, banks of streams and tracks, shallow gullies, stems of shrubs, decaying wood, tree stumps and bamboo grooves.

Ficus religiosa : roots, trunks and upper branches.

Rice terraces : standing crops, stubble and terrace walls.

Small wood immediately above camp.

Small ravine by Tamrang track : rocks and scrub by river.

Gully torrents by Tembe track : banks, rocks, bamboo groves and overhanging trees.

Castanopsis forest : on and amongst trees and in clearings.

Scrubland above *Castanopsis* forest : various habitats including shallow ravines.

SANGHU OAK FOREST AREA. 27° 19′ N., 87° 32′ E. Alt. 7,800–9,300 ft. 2.x.61, 5.xi.61, 28.xi.61, 29.xi.61, 1.xii.61.

Forest, mainly *Quercus lamellosa* and *Q. lineata :* forest floor, decaying wood, on shrubs and trees, rocks and along tracks.

Scrubland below forest.

MILKE BHANJYANG. 27° 19′ N., 87° 31′ E. Alt. 9,300–13,000 ft. 4.xii.61, 29.xii.61.

Rhododendron forest : forest floor, rocks, on trees and along tracks.

Downland above timber line : along tracks.

DOBHAN. 27° 22′ N., 87° 37′ E. Alt. 2,500 ft. 28.i.62–3.ii.62.

Low plateau between Tamur Khola and Maewa Khola : wooded cliffs at river junction and along East bank of Maewa Khola.

East bank of Tamur Khola : sheltered slopes, damp cliffs and gullies.

MEWA KHOLA GORGE CAMP AREA. 27° 33′ N., 87° 36′ E. Alt. 8,000–9,000 ft. 22.i.62–26.i.62.

Dense mixed evergreen forest : forest floor, rocks, walls, on trees and along tracks.

Base of 1,000 ft. rock cliff : numerous habitats.

West low cliff near river.

Smaller collection from various habitats along the route from Dobhan to the Mewa Khola camp, 20.i.62–21.i.62 and 27.i.62–28.i.62.

DHARAN. 26° 49′ N., 87° 16′ E. Alt. c. 1,000 ft. 26.ii.62–27.ii.62.

Sal forest : on trees and in ditches.

TUMLINGTAR. 27° 18′ N., 87° 13′ E. Alt. 1,800 ft. 7.xii.61–26.xii.61.

Plateau : ponds, bamboo groves and isolated trees.

East bank of Sabhaya Khola : wooded cliffs and gullies.

West bank of Sabhaya Khola : wooded cliffs, rocks, gullies and sandy shore.

South bank of Hinwan Khola : cliffs and along Chainpur track.

East bank of Arun Khola : wooded cliffs and gullies.

CHAINPUR. 27° 17′ N., 87° 19′ E. Alt. c. 4,000 ft. 6.xii.61, 7.xii.61–28.xii.61.

Isolated trees and along tracks.

ENTOMOLOGY

Over 21,000 insects were collected and although special attention was paid to the Diptera a wide range of material belonging to other orders, including representatives of the Orthoptera, Dermaptera, Ephemeroptera, Odonata, Neuroptera, Anoplura, Trichoptera, Hemiptera, Isoptera, Lepidoptera, Coleoptera and Hymenoptera, was obtained. With exception of the Odonata, which were particularly abundant over the paddy fields until late October the population of winged insects was not high. The field work began in late September and ended in early February and during this period most of the plants were in seed and failed to attract insects. Moreover, cold winds and frequent frost had by late November resulted in a further reduction of the population in exposed places. These circumstances stimulated a thorough exploration of the deeper ravines and other sheltered localities and an unusually extensive range of small Diptera was collected. Much of this material was collected by sweeping the dense vegetation bordering streams in deep gullies. Had the Expedition been in the field during the flowering season the time would have been almost fully spent in pursuit of the larger flies visiting the blooms and less attention would have been paid to the unexpectedly rich microfauna of the ravines.

Although a systematic study of the material has not yet been made a preliminary examination has revealed interesting affinities with the fauna of the mountainous regions of Burma, Indo-China and Northern Thailand. In localities up to an altitude of about 9,000 ft. palaearctic species were generally few and mostly those with a cosmopolitan distribution. An interesting exception were the coprophagous Sphaeroceridae (Borboridae) which were represented by palaearctic species even at altitudes as low as 1,000 ft.

LOCALITIES

SANGHU BASE CAMP AREA. 27° 21′ N., 87° 33′E. Alt. 5,500–7,000 ft. 2.x.61–4.xii.61, 1.i.62–16.i.62, 11.ii.62–19.ii.62.

Traps containing fermenting bananas and pears.
Fermenting fruits of the Bhor Tree (*Ficus religiosa*) on camp site.
Deep river gorge on Tamrang track : banks and mixed vegetation, dry and spray-splashed rocks.
Standing rice crops and rice stubble.
Herbaceous plants and flowering shrubs along tracks and in gullies.
Shallow ravine below camp site : splashed rocks and banks of stream.
Castanopsis forest : amongst trees and in clearings.
Scrubland above *Castanopsis* forest : amongst *Lycopodium* sp. and shrubs.
Blossoms of *Prunus* sp.
Caked mud in dried pools.
Gully torrents by Tembe track : banks, rocks and amongst overhanging trees.
Small wood immediately above camp.

SANGHU OAK FOREST AREA. 27° 19′ N., 87° 32′ E. Alt. c. 7,800–9,300 ft. 2.xi.61, 26.xi.61, 23.xi.61–4.xii.61, 11.i.62–14.i.62.

Forest, mainly *Quercus lamellosa* and *Q. lineata* : amongst trees in clearings and along tracks.

Scrubland below forest amongst *Lycopodium* sp.

CHAINPUR. 27° 17′ N., 87° 19′ E. Alt. c. 4,000 ft. 6.xii.61.

Around *Ficus religiosa* and on grassy plateau.

TUMLINGTAR. 27° 18′ N., 87° 13′ E. Alt. 1,800 ft. 8.xii.61–25.xii.61.

Traps containing fermenting banana at camp site.

Sandy West shore of Sabhaya Khola : pile of fermenting millet grain, leaves, human excrement and amongst evergreen shrubs.

West bank of Sabhaya Khola : grassy and rock slopes.

Plateau : bare sandy ground and flowering crop of *Guizotia abyssinica*.

East shore of Arun Khola, west of Tumlingtar : dwarf bamboo and evergreen shrubs in ravine, dried up streams and rock strewn mud flats.

DOBHAN. 27° 22′ N., 87° 37′ E. Alt. 2,500 ft. 23.i.62—3.ii.62.

East bank of Tamur Khola : ferns, mixed vegetation and amongst overhanging trees in deep ravine ; mixed vegetation on sheltered slopes.

East bank of Maewa Khola : rice stubble, arid slopes and sheltered slopes with mixed vegetation.

Tamur Khola : spray-splashed rocks.

Level plateau between junction of Tamur Khola and Maewa Khola : flowering shrubs, grasses and mixed vegetation.

ZOOLOGY

Although the zoological programme was concerned primarily with the Micro-arthropoda and Nematoda of soil and forest litter some general collecting was also undertaken and approximately 500 spiders and harvestmen, 800 mites (parasitic and free-living), 30 " other " arthropods, 392 fish, 37 amphibia, 48 reptiles, and 32 mammals were taken. Free living nematodes were collected by the Baermann technique in which small muslin bags of soil are immersed in water held in a glass funnel. The animals move out of the soil into the surrounding water and eventually accumulate in the funnel stem. Soil samples were also taken from arable land and dried for subsequent examination for cyst-forming plant-parasitic species. In addition some helminth parasites of vertebrates were collected.

Much has been written on extraction techniques for the investigation of soil and litter Micro-arthropoda (e.g. Macfadyen 1953) but for the fauna of organic soils and forest litter the only practical device for expedition purposes is some form of desiccation funnel. In this type of apparatus which was originally devised by Berlese (1905), the soil or litter is suspended on a sieve over a funnel and as the material dries the animals move downwards and eventually drop into a tube of preservative. Many recent modifications incorporate certain refinements which are important for quantitative work but almost all of these are unsuitable for expedition purposes as they either require elaborate laboratory facilities or utilise samples too small to yield sufficient material for systematic studies.

Although desiccation funnels have also been used with some success for studies of mineral soil populations there is considerable evidence that in such soils, and particularly in those containing a high proportion of particles belonging to the clay fraction, certain animals either do not respond to the stimulus of desiccation or perish before making their escape (Sheals 1957), and better results are often obtained with a flotation technique. A suitable apparatus is described by Raw (1955). Essentially the process consists of eliminating stones and large plant fragments by washing and sieving and then flooding the fine soil with a magnesium sulphate solution of specific gravity 1·12 in a flotation vessel known as the Ladell. The soil particles are dispersed in the solution by a stream of air led in from below, and, after settling, the animals and plant debris on the surface of the solution are collected by decanting on to a suitable sieve. A further separation of animals from plant debris is possible but this part of the process cannot be carried out without good laboratory facilities.

The bulk of the Micro-arthropoda was collected by means of a simple desiccation technique. Plastic funnels, 8½ in. in diameter, were used and the material under examination was carried on a circle of metal gauze 6¼ in. in diameter with a regular square mesh of 3 mm. Fifty-two funnels were set up on a bamboo framework in the Dharam Sala and a small battery of 8 funnels, used for the examination of dung, was accommodated in a canvas shelter. Paraffin pressure lamps were suspended over the indoor funnel assembly and the soil and litter samples were left on the funnels for at least 10 days. A series of mineral soil samples from grazed turf plots and rice terraces was examined by means of a flotation technique based substantially on the apparatus described by Raw (op. cit.) but modified for operation with limited facilities. The initial washing process was carried out with a 7-mesh sieve into plastic bowls, using jets of water from a hand-operated pump, and the soil was dispersed in the flotation vessel with a stream of air from a motor car foot pump. The finest sieve used had a regular square mesh of 152μ (100 mesh B.S.S.). No attempt was made to separate animals from the plant debris in the " float ", consequently many extracts are " dirty " and sorting is likely to be tedious. Nevertheless the use of flotation appears to have been justified, for a preliminary examination has revealed the presence of lightly sclerotized Acari, forms which are often difficult to obtain with desiccation methods.

In addition to obtaining material for systematic studies the micro-arthropod and nematode surveys were undertaken with a view to gathering ecological and zoogeographical data. In this connection it was felt that quantitative assessments would be useful and the numbers of individuals in the samples are being recorded. Population comparisons however will of necessity be made on a proportional basis for, owing to the difficulty of standardizing samples of the various soils and litter studied and the errors inherent in the extraction techniques, absolute numbers have little meaning. Many of the habitats studied were sampled repeatedly, not so much with a view to detailed phenological studies, but rather to obtain an adequate series of developmental instars and to obtain some replication for comparisons.

LOCALITIES

SANGHU BASE CAMP AREA. 27° 21′ N., 87° 33′ E. Alt. 5,500–7,000 ft. 2.x.61–4.xii.61, 1.i.62–16.i.62, 1.ii.62–17.iii.62.

Various habitats including mosses, soil and detritus on boulders, around trees and in small gullies.

Standing rice crops and walls of terraces.

Rice stubble ; soil and litter.

Cattle dung.

Ficus religiosa : tree-hole debris and soil round roots.

Surface and deeper soil of grazed turf plots (examined for micro-arthropods by both flotation and desiccation-funnels techniques).

Castanopsis forest : tree trunks, bark, leaf litter, surface and deeper soil, decaying wood and mosses.

Scrubland above *Castanopsis* forest : soil and litter.

Small wood immediately above camp-site.

Deep river gorge on Tamrang track : soil, litter, plant root systems, soil round roots of ferns and clinging to rocky cliffs.

SANGHU OAK FOREST AREA. 27° 19′ N., 87° 32′ E. Alt. 7,800—9,300 ft. 16.x.61, 26.x.61, 17.i.62.

Dense evergreen oak forest (*Quercus lamellosa* and *Q. lineata* dominating) : litter, surface and deeper soil, bark, mosses, liverworts and lichens on boulders and trees, decaying wood, tree-hole debris.

Forest clearing : soil of grazed mossy turf and moss alone.

MILKE BHANJYANG. 27° 19′ N., 87° 31′ E. Alt. 9,300–13,000 ft. 12.x.61, 17.xi.61, 22.xi.61–24.xi.61, 2.xii.61, 14.i.62 ; 17.i.62, 28.ii.62.

Rhododendron forest : litter ; surface and deeper soil ; mosses, liverworts and lichens on trees and boulders ; decaying wood.

Alpine turf above forest : soil examined to a depth of 9 in. with both flotation and desiccation funnel techniques for micro-arthropods and replicates examined for nematodes in two sub-samples, surface—5 in. and 5 in.–9 in. Mosses, lichens and liverworts in same general area, on stones and boulders.

Top of Milke Danra North of Milke Bhanjyang : grass and soil, surface soil round roots of rhododendrons, surface litter, moss, hard frozen soil (for nematodes only).

TOPKE GOLA. 27° 3′ N., 87° 35′ E. Alt. 12,500–13,000 ft. 27.x.61–28.x.61.

Small coniferous forest : litter, soil, tree-hole debris.

Rhododendron forest : litter, soil, decaying wood, mosses and organic soil on large boulder, tree-hole debris.

Juniper scrub (*Juniperus* (?)*squamata*) : litter and soil.

Alpine turf : surface soil.

SURKENAGI. 27° 14′ N., 87° 50′ E. Alt. c. 8,000 ft. 10.xi.61.

Rhododendron/Oak forest : litter, surface soil, deeper soil, tree-hole debris, soil of turf in clearing.

MEMENG. 27° 12′ N., 87° 56′ E. Alt. c. 5,000 ft. 11.xi.61.
Organic soil in rock crevices and soil of riverside turf.

SOLE. 27° 10′ N., 87° 56′ E. Alt. c. 8,000 ft. 12.xi.61.
Evergreen oak forest : litter, surface soil, tree-hole debris.

SANDAKPHU. 27° 06′ N., 88° 01′ E. Alt. 12,000 ft. 13.xi.61.
Rhododendron/conifer scrub : surface soil.
Dwarf *Rhododendron* copse : surface soil.

DHARAN. 26° 49′ N., 87° 16′ E. Alt. c. 1,000 ft. 21.xi.61, 27.ii.62.
Sal forest : surface soil, decaying wood, moss on bank of stream.
Rice stubble : surface soil.

PHUSRE. 26° 50′ N., 87° 17′ E. Alt. c. 3,000 ft. 22.xi.61.
Moss on dry bank, litter in scrubland on side of track.

MULNGHAT. 26° 56′ N., 87° 19′ E. Alt. c. 1,000 ft. 23.xi.61.
Grazed turf : surface soil.
Moss and litter under bushes near stream bed.

POPTI LA ROUTE. 27° 47′ N., 87° 21′ E. Alt. 10,800 ft. 21.xii.61.
Rhododendron/Conifer forest : litter, soil, mosses on trees and boulders, decaying wood, tree-hole debris.
Cardocrinum giganteum : soil around roots.
Evergreen Oak forest : litter, soil and decaying wood.

NUM. 27° 33′ N., 87° 18′ E. Alt. c. 5,000 ft. 15.xii.61.
Rice stubble : surface soil.
Grazed turf : surface and deeper soil.
Castanopsis forest : litter and surface soil.

DHOJE. 27° 26′ N., 87° 13′ E. Alt. c. 6,500 ft. 15.xii.61.
Grazed turf : surface soil.
Ungrazed grassland : surface soil.

DHANRGAON. 27° 28′ N., 87° 15′ E. Alt. c. 7,000 ft. 15.xii.61.
Mixed woodland, mainly oak : litter.
Mosses and soil on old stone walls.

TUMLINGTAR. 27° 18′ N., 87° 13′ E. Alt. c. 1,800 ft. 21.xii.61–25.xii.61.
Immediate area of camp site : rotting banana on ground, grass roots and soil, soil round bamboo, moss, rotting wood.
Hinwan Khola : damp grazed turf surface soil, soil from beneath rotting maize straw and straw itself.
Sabhaya Khola : shallow dammed lagoon with fish trap and very heavy growth of algae, boulders along edge of river.

DOBHAN. 27° 22′ N., 87° 37′ E. Alt. 2,500 ft. 25.i.62–1.ii.62.
Taplejung bank of Tamur Khola : damp, muddy soil, from grassy area and also under trees ; bottom litter and soil in small wood ; mosses.
Plateau between junction of Tamur and Maewa Kholas : surface soil and grass roots, surface litter beneath and soil from around roots of scattered bushes.

Tamur Khola about 1–2 hours march South of Dobhan : forest bottom litter, turf and mosses.

ANBUNG. 27° 16′ N., 87° 42′ E. Alt. c. 2,500–3,000 ft. 31.i.62–2.ii.62.
Pinus roxburghii woodland : litter.
Deep gully : plant debris and soil.
Mixed woodland, mainly *Castanopsis :* litter and soil.
Ridge above Hangpang, Alt. c. 6,000 ft. : Scrubland, mainly *Pinus roxburghii :* litter and soil.
Junction of Tamur and Kabeli Kholas : forest bottom litter, soil and mosses.

HATIA. 27° 44′ N., 87° 21′ E. Alt. c. 7,500 ft. 23.xii.61.
Evergreen Oak forest : litter and surface soil.

WALUNGCHUNG GOLA. 27° 41′ N., 87° 47′ E. Alt. c. 12,700 ft. 2.ii.62.
Rhododendron/conifer forest : litter, soil, moss on rocks.
Coniferous forest : bottom litter.

SELAP. 27° 38′ N., 87° 49′ E. Alt. 10,000–10,300 ft. 4.ii.62.
Rhododendron forest : litter, and moss on rocks.
Rhododendron/*Berberis* scrub : litter.

LUNGTHUNG. 27° 33′ N., 87° 48′ E. Alt. c. 6,400 ft. 5.ii.62.
Rice stubble : surface soil.

HELLOK. 27° 31′ N., 87° 48′ E. Alt. 6,100 ft. 5.ii.62.
Mixed forest, mainly oak : litter and surface soil.

DHANKUTA. 26° 59′ N., 87° 21′ E. Alt. c. 4,000 ft. 3.iii.62.
Coniferous forest : litter.

HILE. 27° 01′ N., 87° 19′ E. Alt. c. 6,000 ft. 3.iii.62.
Soil from cultivated terrace, no plant cover.
Grazed damp turf : surface soil.

CHITRE. 27° 07′ N., 87° 24′ E. Alt. c. 7,000 ft. 4.iii.62.
Mixed forest, mainly oak : surface litter.

PERSONNEL

J. G. Sheals, zoologist, leader first phase ; W. G. Inglis, zoologist, leader second phase ; R. L. Coe, entomologist, deputy leader ; A. H. Norkett, botanist, K. H. Hyatt, zoologist ; T. Le M. Spring Smyth, administrative officer ; and B. P. Sharma, liaison officer.

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PLATE I

The Expedition Base Camp at Sanghu. The rest house (left) facing the tents was equipped as a laboratory-cum-messroom.

PLATE 1

PLATE 2

Sanghu Base Camp. Part of the battery of " outdoor " funnels used for the extraction of arthropods from dung, etc.

PLATE 3

Sanghu Base Camp. Flotation extraction : decanting the " float " on to a 100 mesh sieve.

PLATE 4

The Tamur River below Dobhan, looking North.

PLATE 4

PLATE 5

Maewa Khola : evergreen oak forest above Sanghu Base Camp.

PLATE 6

Milke Danra : downland and rhododendron forests.

PLATE 6

PLATE 7

Jaljale Himal at Topke Gola.

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Department of Zoology, British Museum (Natural History)

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A PRELIMINARY REVISION OF THE INDO-PACIFIC ALOSINAE (PISCES: CLUPEIDAE)

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THE WEST AFRICAN GENUS *Ethmalosa*	153

ABSTRACT

Hilsa Regan and *Gudusia* Fowler are the only two Indo-Pacific genera of the clupeid subfamily Alosinae. New systematic characters are examined and the genus *Hilsa* is divided into the subgenera *Hilsa* (*H. kelee*) and *Tenualosa* (*H. ilisha*, *H. reevesii*, *H. macrura* and *H. toli*). *Macrura* van Hasselt is not a senior synonym of *Hilsa*. Two species of *Gudusia* are recognized (*G. chapra* and *G. variegata*).

The position of the West African genus *Ethmalosa* Regan is examined ; on present evidence, *Ethmalosa* is considered intermediate between the Indo-Pacific and the Atlantic Alosinae.

INTRODUCTION

The last revision of the Indo-Pacific Alosinae was that of Regan (1917), although Fowler (1941) listed all Indo-Pacific species and gave extensive synonymies. The more important species, such as *Hilsa ilisha*, have been fairly well studied, but others are little known and are poorly represented in museum collections. The material available has, however, enabled me to correct certain errors in previous synonymies and, using characters not employed before, to define the species more precisely. At the same time these characters have renewed the problem of the true phyletic relationships, both within the Indo-Pacific group, and between them and the Eastern Atlantic and New World groups. Such features as the development of a cleithral lobe or the presence of a striated fronto-parietal wedge appear in clupeid genera which otherwise are not closely related, and until the significance of such characters within the whole family can be reviewed, their importance relative to other characters within the Alosinae can only be guessed at. For this reason, and also because of the lack of specimens in some species, this study can represent no more than a preliminary revision.

Regan (*loc. cit.*) treated as a single group those clupeid genera which have a distinct notch in the middle of the upper jaws, stating that " all these fishes appear either to be migratory, entering rivers to spawn in fresh or brackish water, or are permanently fluviatile." Regan then divided this group into those genera in which the epibranchial gillrakers near the angle of the arch fold down over the gillrakers of the ceratobranchial ; and those in which the gillrakers near the angle of the arch lie roughly in the same plane. In the first section he placed the genera *Alosa, Caspialosa, Brevoortia, Pomolobus* and *Ethmidium* ; and in the second section he placed the gizzard shads and the genera *Hilsa, Gudusia* and *Ethmalosa*. Svetovidov (1952) placed all these genera in the subfamily Alosinae, except the gizzard shads, which he removed to a separate subfamily, the Dorosomatinae.

Regan's gillraker character would seem to be a useful means of dividing the Alosinae into two tribes. It is supported by a difference in pelvic finray number, the Indo-Pacific genera having 8 rays, and the New World, Eastern Atlantic and Mediterranean genera having 7 or 9. However, the West African genus *Ethmalosa* appears to be as closely allied to the Atlantic Alosinae as it is to those of the Indo-Pacific. This is discussed in more detail later.

Both *Hilsa* and *Gudusia* contribute to important fisheries, and in Bengal, *Hilsa ilisha* is the most popular of all marine fishes (Hora 1954). The *Hilsa ilisha* fisheries of India have received considerable attention among Indian workers, and much of the available biological knowledge has been summarised by Pillay and Rosa (1957). *H. ilisha*, and probably all other species, is anadromous, but land-locked populations exist (e.g. in Chilka Lake—see Mitra and Devasandarum 1954). *Gudusia* on the other hand is purely fluviatile. *Hilsa* has a wide distribution, from Natal to China, but *Gudusia* is restricted to the rivers of India and Burma.

Regan (*loc. cit.*) used the form of the fronto-parietal ridges to divide his seven species of *Hilsa* into two groups. I have here followed Fowler (1934, 1941) in using this character to support a subgeneric division within *Hilsa*. Further characters are discussed which reinforce such a division.

The following classification has been adopted here :—

- Subfamily Alosinae (Shads)
  - Genus *Hilsa*
    - Subgenus *Hilsa* (*H. kelee*)
    - Subgenus *Tenualosa* (*H. ilisha, H. reevesii, H. toli, H. macrura*)
  - Genus *Gudusia* (*G. chapra, G. variegata*)

Note on measurements used.

LENGTH : standard length used throughout.

HEAD LENGTH : the longest measurement, from premaxillary symphysis to posterior border of suboperculum, occasionally to posterior border of operculum.

MAXILLA LENGTH : from premaxillary symphysis to maxilla tip.

PREORBITAL DISTANCE : this measurement *includes* the eye, i.e. premaxillary symphysis to posterior border of eye.

CAUDAL LENGTH : length of unscaled portion of lower lobe.

SYSTEMATIC CHARACTERS

(a) *Fronto-parietal ridges.*

The two forms of fronto-parietal ridge found in *Hilsa* are shown in Figure 1A and B. In the *Hilsa* form (1A) the wedge-shaped ridges are exposed and bear numerous longitudinal striae. In the median area between the two wedges, the frontals are covered by a thin layer of skin. The supra-occipital is exposed for some distance anteriorly, between the posterior tips of the frontals ; posteriorly it is raised into a median, transverse ridge.

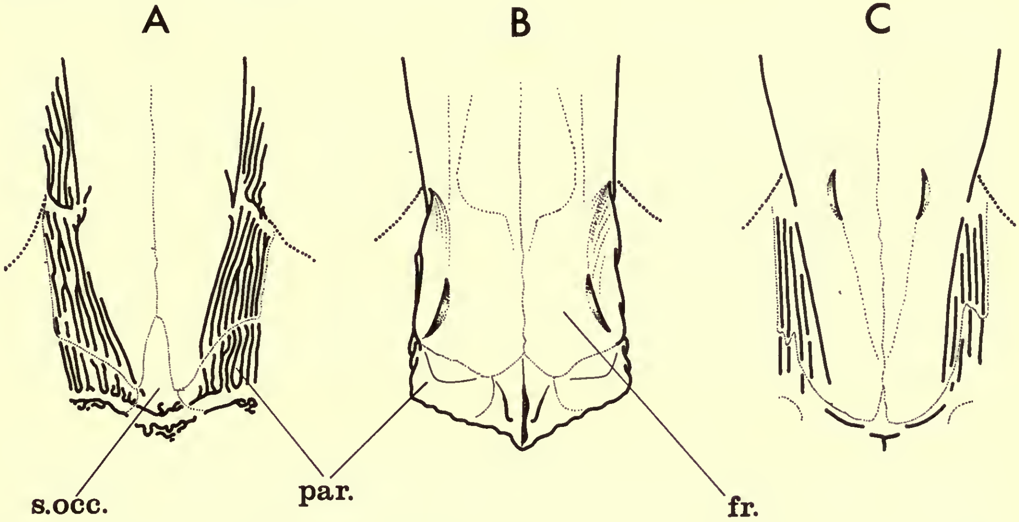


FIG. 1. Fronto-parietal striation patterns (dorsal view of posterior part of head, skin removed). A. "*Hilsa*" pattern (180 mm. fish, syntype of *Clupea durbanensis* = *H. kelee*). B. "*Tenualosa*" pattern (210 mm. fish, *H. ilisha*). C. "*Gudusia*" pattern (150 mm. fish, *G. variegata*).
s. occ. supra-occipital. *par.* parietal. *fr.* frontal.

In the *Tenualosa* form (1B) there is no wedge-shaped striated fronto-parietal ridge, although the lateral margins of the frontals in this area may form one or two longitudinal grooves. The entire region is covered by a thick layer of skin, but the lateral margins of the frontals are sometimes visible. The supra-occipital is partly exposed anteriorly, as in the *Hilsa* form ; posteriorly it bears a longitudinal ridge, flanked by two smaller longitudinal ridges.

In *Gudusia* (Figure 1C) the fronto-parietal ridges are striated and exposed and resemble those of the *Hilsa* form. However, the striae are not continued forward along the frontals to the same extent as in the *Hilsa* form.

The difference between the two subgenera of *Hilsa* in fronto-parietal ridge form is in fact greater than that which separates the clupeid genus *Sardinella* from either *Harengula* (Western Atlantic) or *Herklotsichthys* (Indo-Pacific). In these genera the fronto-parietal character appears to hold genuine phyletic significance (Whitehead, 1964a), and it is therefore possible that the two groups of *Hilsa* might be more correctly allocated to separate genera also. For the time being, however, and until this character can be studied in other clupeid genera, I have preferred to maintain a subgeneric division only.

(b) *Maxillary bones*

In the genus *Hilsa* there are two supra-maxillae lying along the dorsal margin of the maxilla. The second or posterior supra-maxilla is expanded and paddle-shaped posteriorly and pointed and shaft-like anteriorly. There is some variation in the shape of the expanded portion (smaller than in other species in *H. ilisha* and *H. reevesii*), but there is no trenchant difference in size or shape between the two subgenera. The first or anterior supra-maxilla, however, is slightly deeper in *Hilsa* (*Hilsa*) than in *Hilsa* (*Tenualosa*).

The expanded (posterior) portion of the maxilla is similar in general shape in both subgenera, but is rather longer in *H. ilisha* and *H. reevesii*. In the subgenus *Hilsa* (*Hilsa*), however, there are four to six longitudinal ridges on this expanded portion (Figure 2A), but these are absent in *Hilsa* (*Tenualosa*) (Figure 2B and C). Occasionally species of the latter subgenus may have one or more fine grooves in the maxilla, but these are never developed into ridges.

H. macrura has a much shorter maxilla than have other species (Figure 2B), the tip not passing the vertical through the pupil of the eye.

In *Gudusia* the maxilla and supra-maxillae closely resemble those of *Hilsa* (*Tenualosa*), especially *H.* (*T.*) *toli*.

(c) *Cleithral lobe.*

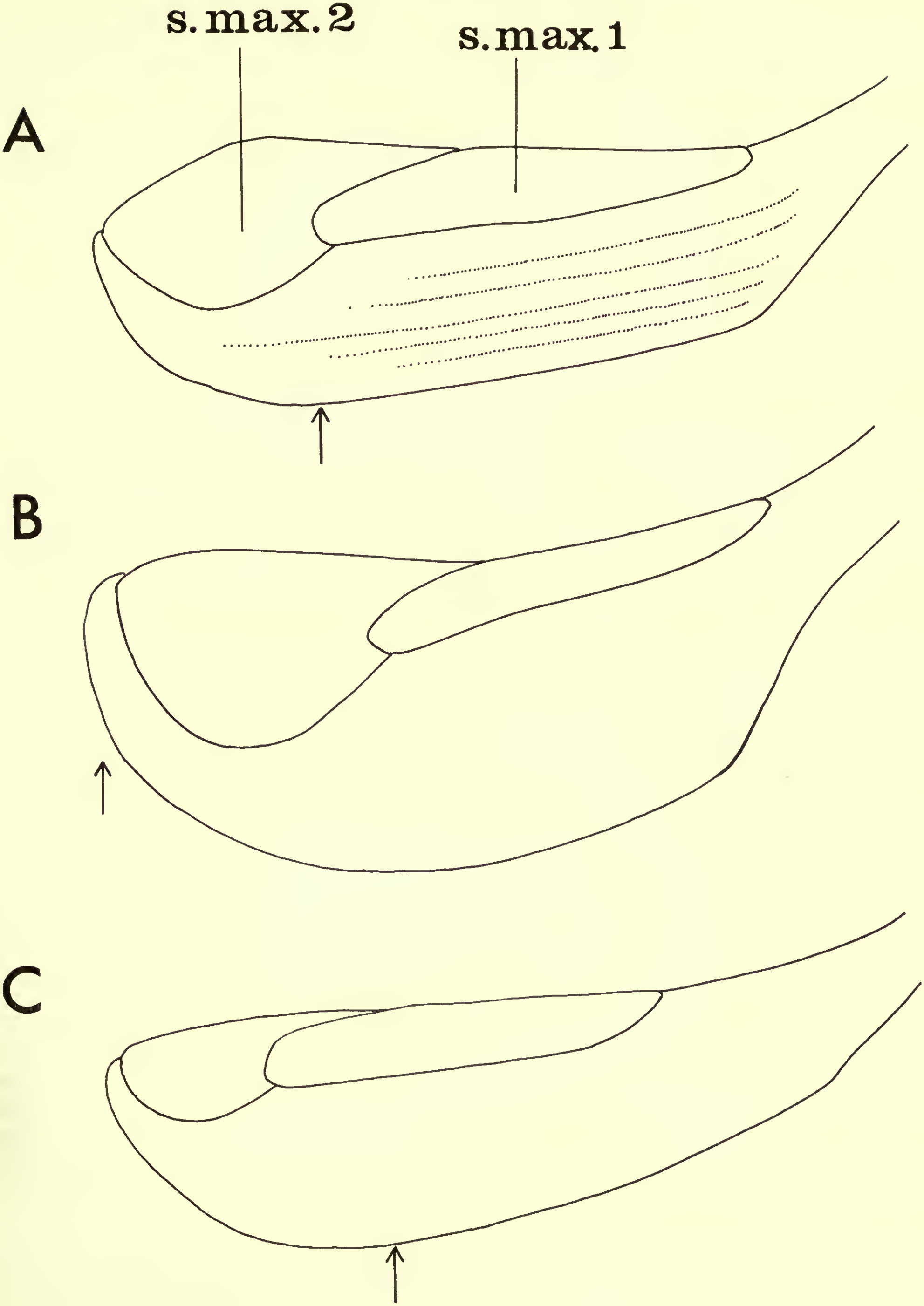
In clupeid fishes the tissue covering the anterior margin of the cleithrum may be expanded in places, thus giving the gill cavity an irregular posterior outline. In some genera, for example in *Sardinella*, there is a fleshy lobe at the postero-ventral angle of the gill opening, just above the base of the pectoral fin. This lobe, which occurs in some genera of the Dussumieriidae, I have elsewhere termed the cleithral ' flap ' (Whitehead, 1963), but ' lobe ' is perhaps a better term.

In the subgenus *Hilsa*, the cleithral lobe is well developed, breaking the posterior outline of the gill opening and projecting sufficiently to cover the underlying filaments of all but the first gill arch (Figure 3A). In front of the cleithral lobe there is an oblique groove. The final two branchiostegal rays cover this groove.

In species of the subgenus *Tenualosa*, the cleithral lobe projects little into the gill cavity and in most cases barely interrupts the cleithral outline (Figure 3B). In

---

FIG. 2. Maxillary bones in species of *Hilsa* (right side). Arrow indicates vertical through eye centre. A. *Hilsa kelee* (syntype of *Clupea durbanensis*, 180 mm.). B. *Hilsa macrura* (160 mm. specimen, Sarawak). C. *Hilsa ilisha* (210 mm. specimen, Calcutta). *s. max.*1 anterior supra-maxilla. *s. max.*2 posterior supra-maxilla.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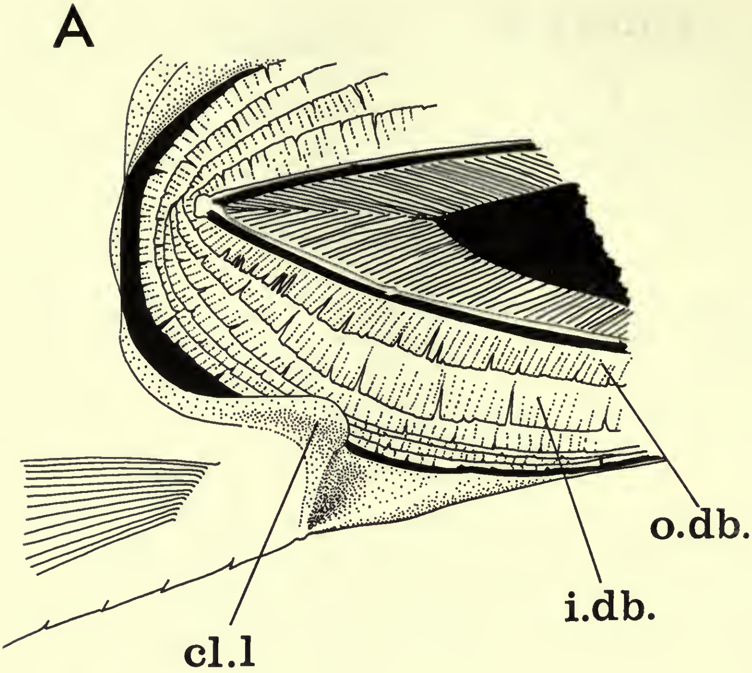
s. max. 1
A
B
C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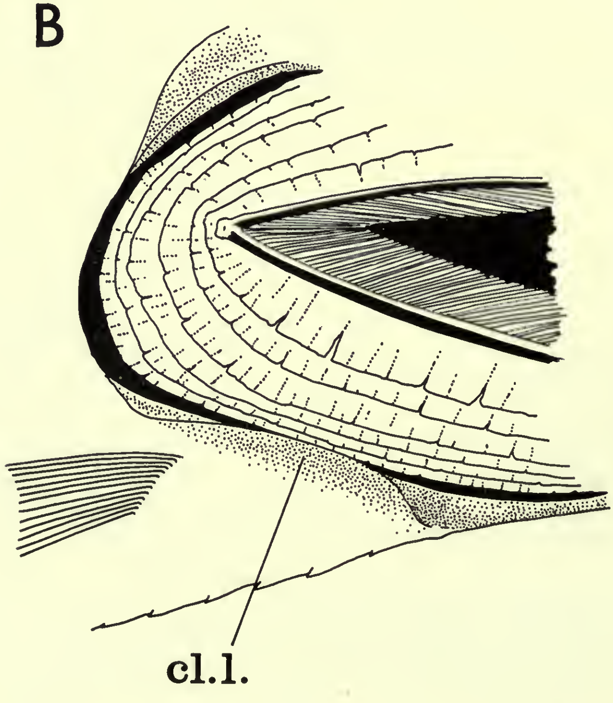
B
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H. macrura the cleithral lobe is rather more developed, but it never projects into the gill chamber to the same extent as in *H. kelee*. In *H. macrura* and other species of *Hilsa* (*Tenualosa*) the groove in front of the cleithral lobe is either very shallow or absent.

This character is less apparent in juvenile fishes, and in small specimens of *Hilsa* (of about 50 mm.) the cleithral lobe is similar and poorly developed in both subgenera.

In *Gudusia* the cleithral lobe is slightly developed, and resembles that of *H. macrura*, i.e. it is intermediate in size between *Hilsa* (*Hilsa*) and *Hilsa* (*Tenualosa*).

(d) *Gill filaments.*

In the subgenus *Hilsa*, the gill filaments of the outer hemibranch of the first gill arch are very short, barely half the length of those of the inner hemibranch. In species of *Hilsa* (*Tenualosa*), the filaments of the outer hemibranch are more than a half the length of those of the inner hemibranch (Figure 3A and B).

In juveniles, the outer filaments in species of *Hilsa* (*Tenualosa*), tend to be relatively shorter, but the distinction between the two subgenera is normally obvious, and especially if comparative material is available.

Gudusia resembles *Hilsa* (*Tenualosa*), having the filaments of the outer hemibranch more than half the length of those of the inner hemibranch.

(e) *Gillrakers.*

In the subgenus *Hilsa*, the gillrakers on the second, third and fourth arches are curled outwards (Figure 4B). At the tip of the raker there is a small knob which, *in situ*, rests against that of its neighbours so that the raker tips are held in line. The inner (convex) margin of each raker bears a series of short spines or serrae (about 100 on each raker). Along the outer margin (concave) there is a thin flange of skin, expanded on some rakers, narrow on others.

The lower gillrakers of the first arch in the subgenus *Hilsa* are longer than the corresponding gill filaments, and in fishes over 80 mm. standard length they exceed eye diameter (three-quarter eye diameter at 50 mm.).

In the subgenus *Tenualosa* the gillrakers on all arches are straight or very slightly curved (Figure 4A). The serrae are slightly fewer than in *Hilsa* and there is no flange of skin along the outer margin of the raker. The tips of the rakers are pointed, except in *H. macrura*.

The lower gillrakers of the first arch in *Hilsa* (*Tenualosa*) are as long as those in *Hilsa* (*Hilsa*) except in the case of *H. macrura* (Figure 4C), where they are about half the length of the corresponding gill filaments (less than the diameter of the pupil at 150 mm. standard length).

In *Gudusia* the gillrakers are straight or slightly curved and resemble those of *H. ilisha* in form and length.

FIG. 3. Cleithral profile and gill arches (right side, operculum removed). A. *Hilsa kelee* (syntype of *Clupea durbanensis*, 180 mm.). B. *Hilsa ilisha* (210 mm. specimen, Calcutta). *cl. l.* cleithral lobe. *o. db.* outer hemibranch of 1st arch. *i. db.* inner hemibranch of 1st arch.

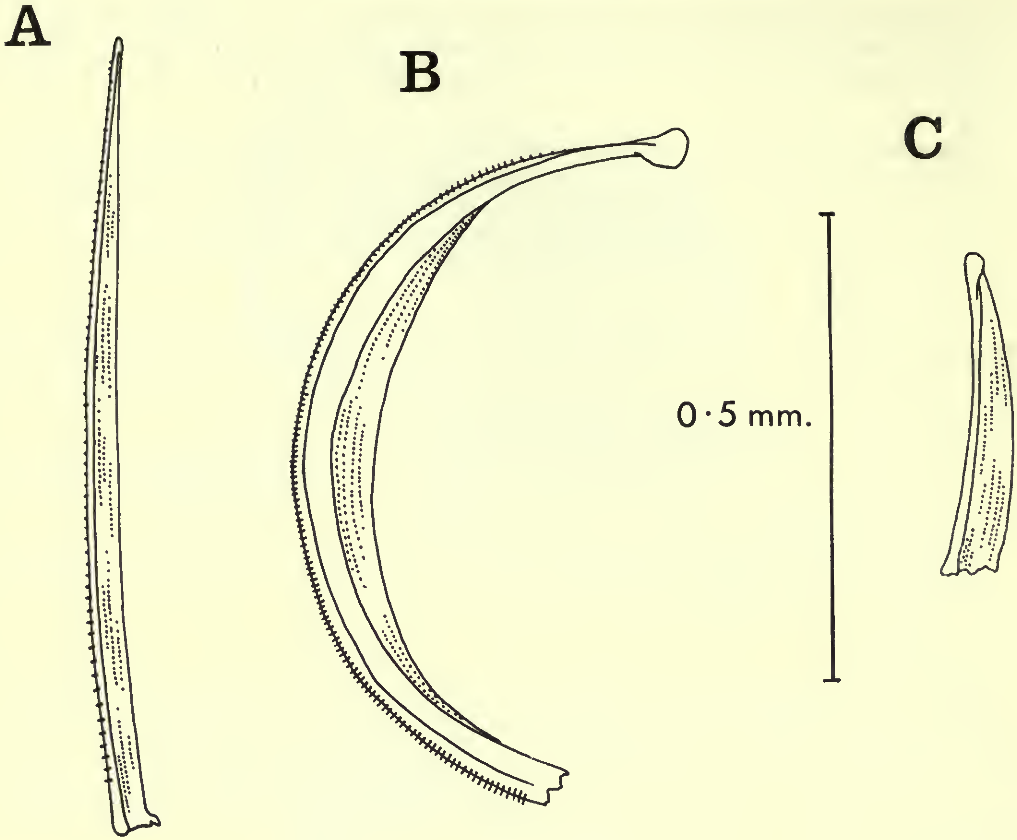

FIG. 4. Gillrakers from lower part of first arch in species of *Hilsa*. A. *Hilsa ilisha* (215 mm. fish). B. *Hilsa kelee* (syntype of *Clupea durbanensis*, 180 mm.). C. *Hilsa macrura* (155 mm. fish).

(f) *Opercular bones.*

In *Gudusia* the lower margin of the operculum rises more steeply than in either *Hilsa* (*Hilsa*) or *Hilsa* (*Tenualosa*) (Figure 5A and B). If the line of the lower operculum margin is produced posteriorly, it intersects the dorsal body profile near or in front of the dorsal origin in *Gudusia*, but behind this point in *Hilsa*. In *Gudusia* the suboperculum is in consequence less rectangular.

Within *Hilsa* (*Tenualosa*) there is some variation in the shape of the operculum and suboperculum. In *H. macrura* the latter is almost rectangular and the lower border of the operculum is near the horizontal. *H. toli* and *H. ilisha* resemble *H. kelee* (Figure 5A). In *H. reevesii* the operculum and suboperculum are broader than in other species, the length of the suboperculum (upper exposed margin) being contained less than twice in the height of the operculum (more than twice in all other species of *Hilsa*, but not in *Gudusia*).

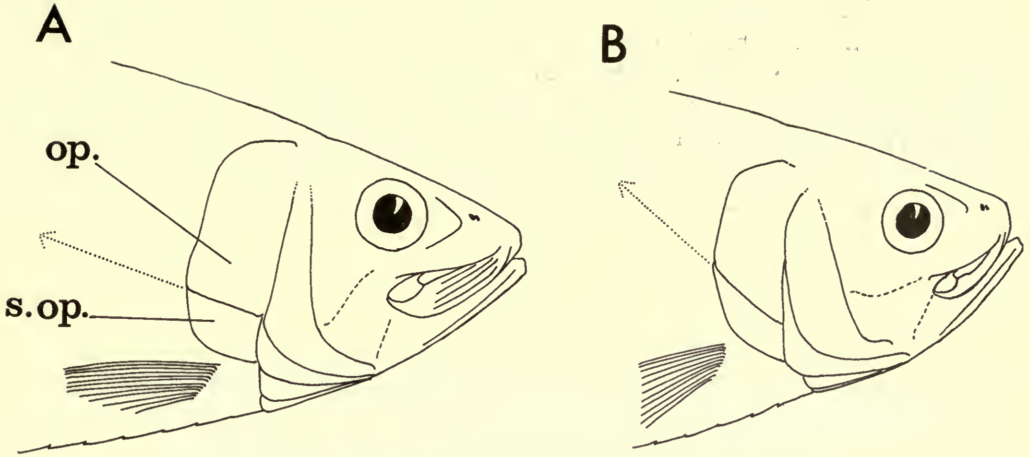

FIG. 5. Opercular bones in *Hilsa* and *Gudusia*. Dotted arrow indicates line projected along upper (exposed) margin of sub-operculum. A. *Hilsa kelee* (syntype of *H. durbanensis*, 180 mm.). B. *Gudusia variegata* (150 mm. fish).

op. operculum. *s. op*. sub-operculum.

(g) *Pseudobranchiae.*

Pseudobranchiae are present in all genera of the Alosinae. In *Hilsa* there are slight interspecific differences in the shape of the pseudobranch, and one of these is sufficiently marked to be commented on.

The pseudobranch in *H. ilisha* and *H. reevesii* differs from that of all other species of *Hilsa* in having a slightly longer base and a more attenuated appearance (Figure 6A). Although the longest pseudobranchial filaments are as long as those in other species, filament length decreases more gradually posteriorly (*cf* Figure 6A and B). The difference between these two forms is not great, but is easily apparent when a comparison can be made. In addition, *H. ilisha* and *H. reevesii* have a distinct groove below the base of the pseudobranch, into which the tips of the gillrakers of the first arch fit. A groove is absent in *H. toli* and *H. macrura*, but occurs in *H. kelee*.

The pseudobranch in *Gudusia* is attenuated and resembles that of *H. ilisha*. A groove is present.

THE ALOSINAE OF THE INDO-PACIFIC

While *Hilsa kelee* is sufficiently distinct from the remaining species of *Hilsa* to be separated subgenerically (or even generically), *Gudusia* combines characters from both of the subgenera, but at the same time possesses its own distinctive features. The question arises whether the degree of affinity between the three taxa, *Hilsa* (*Hilsa*), *Hilsa* (*Tenualosa*) and *Gudusia*, is equal or whether one has diverged further from the other two. The distinctive characters of each are shown in Table I.

Hilsa (*Hilsa*) is distinguished from *Gudusia* on seven counts, and from *Hilsa* (*Tenualosa*) on five, while the latter is distinguished from *Gudusia* on four counts. But obviously some characters have more phyletic importance than others. The fronto-parietal character links *Hilsa* (*Hilsa*) with *Gudusia*, but in other respects *Gudusia* would appear to have evolved as a fluviatile offshoot of *Hilsa* (*Tenualosa*), the increase in scale number being linked with this change of habitat. If *Gudusia* is recognised as a separate genus, then there is good reason for separating *Hilsa*

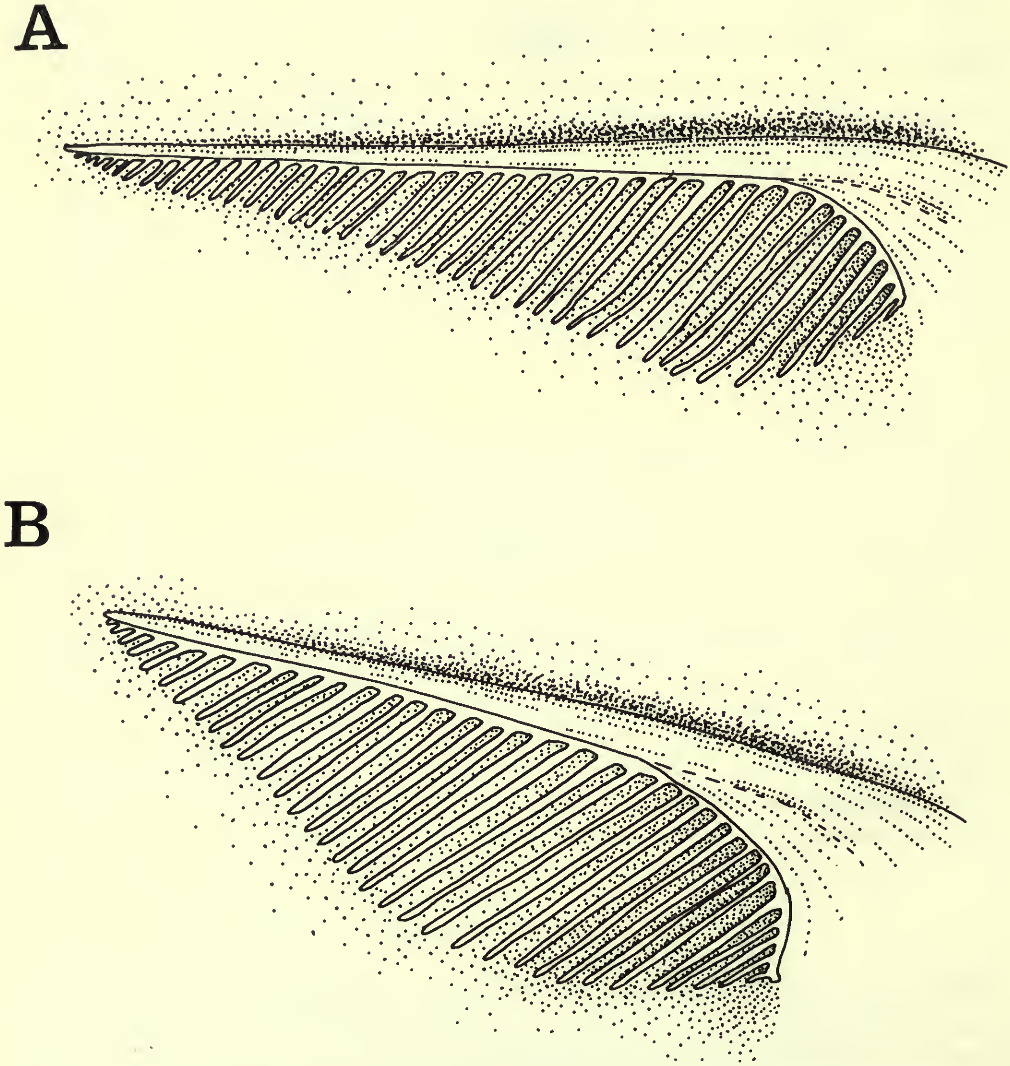

Fig. 6. Pseudobranch shape in species of *Hilsa* (right side, with thickened lower edge shown uppermost). A groove present along lower edge in both species. A. *Hilsa ilisha*. B. *Hilsa kelee*.

(*Tenualosa*) at generic level too. Alternatively, each of the three taxa might be accorded subgeneric rank. Much depends on the importance accorded to the development of the fronto-parietal sculpture. Under these circumstances, I have preferred to leave *Gudusia* as a separate genus and to retain the *Tenualosa* forms within *Hilsa* for the time being. Fowler(1958) proposed a new subfamily, the Gudusiinae, defined to include *Gudusia* alone, but this does not seem to be justified.

TABLE I

Hilsa (*Hilsa*)	*Hilsa* (*Tenualosa*)	*Gudusia*
Curled gillrakers.	No fronto-parietal striated wedge.	Small and numerous scales.
Large cleithral lobe.		Steeply rising operculum lower border.
Ridged maxilla. Short outer hemibranch on first arch.		Fluviatile habit

Diagnosis.

Indo-Pacific clupeid fishes with a distinct notch in the middle of the upper jaw and with the gillrakers of the epibranchial of the first arch not folding over those of the ceratobranchial. Gillrakers present on inner face of epibranchial of third arch. Pseudobranch present. Body compressed, with pre- and post-pelvic scutes, but no pre-dorsal scutes. Two supra-maxillae, the posterior one expanded ; no hypomaxilla. Operculum smooth or with a few fine vertical striae. Anal fin moderate 18–29 rays, of which the last two are normal and not enlarged. Pelvic fins present, 8-rayed, not reduced in size ; pelvic origin a little behind dorsal origin. No alar scales on caudal fin. Purely riverine (*Gudusia*) or marine and anadromous (*Hilsa*). From Natal to China.

KEY TO THE GENERA AND SUBGENERA

I Scales large, 40–50 in lateral series ; lower edge of operculum as in Figure 5A ; marine, anadromous . . . . **Hilsa** Regan

a Fronto-parietal ridges exposed, bearing many longitudinal striae (Figure 1A) ; exposed part of expanded portion of maxilla with 4–6 longitudinal ridges (Figure 2A) ; cleithral lobe prominent (Figure 3A) ; gill filaments of outer hemibranch on first arch not more than half length of inner hemibranch ; gillrakers on second, third and fourth arches curled outwards (Figure 4B) subgenus **Hilsa**

b Fronto-parietal ridges covered by skin, a few or no striae present (Figure 1B) ; maxilla smooth on exposed part of expanded portion (Figure 2B) ; cleithral lobe not prominent (Figure 3B) ; gill filaments of outer hemibranch on first arch more than half length of those on inner hemibranch ; gillrakers on second, third and fourth arches straight or very slightly curved (Figure 4A and C) subgenus **Tenualosa**

II Scales small, 80–120 in lateral series ; lower edge of operculum steeply inclined as in Figure 5B ; fluviatile. . . . . **Gudusia** Fowler

Hilsa Regan

Hilsa Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 303 (type *Paralosa durbanensis* Regan, *ex*. Durban).

Paralosa Regan, 1916, *Ann. Durban Mus.*, **1** (3) : 167 (type *Clupea durbanensis* Regan) (*non* Bleeker 1872, see below).

Tenualosa Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 (type *Alosa reevesii* Richardson *ex* China).

Macrura Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 626 (type *Clupea kelee* Cuvier) (see note on *Macrura* van Hasselt).

Indo-Pacific alosinid fishes with moderate scales, 40–50 in lateral series, 12–20 in transverse series ; scales adherent. Suboperculum rectangular, or subrectangular, its junction with the operculum, if produced, cutting the dorsal profile in the middle of the dorsal base or behind (Figure 5A).

Branchiostegal rays 5–6. Gillrakers numerous, 60–220, slender. Dorsal rays 17–20, pelvic 8, anal 17–22. Ventral scutes, 16–19 pre-pelvic and 11–15 post-pelvic.

Two subgenera and five species recognised here, from coasts and rivers from Natal to China.

Note on synonymy.

Fowler (1941) believed *Macrura* van Hasselt 1823 to be the earliest available generic name for those clupeid fishes related to the ' Keelee ' of Russell (1803, p. 75, pl. 195), i.e. *kanagurta, ilisha, toli*, etc. Smith (1949, p. 90) followed Fowler's example, as also did Whitley (1948 and 1953) and Munro (1955). Indian workers, on the other hand, have generally placed these species in *Hilsa* Regan 1917. Regan (1916) proposed *Paralosa* for those Indo-Pacific species placed by Bleeker (1872) in *Alosa*. Later, (Regan 1917) he created *Hilsa* to replace his monotypic *Paralosa*, presumably on grounds of homonymy, although this is not stated ; *Paralosa* Bleeker 1872 is in fact a junior synonym of *Sardinella* (Whitehead 1964a). Since the works of Fowler, Smith and Whitley are quite extensively used, and since the original indication of *Macrura* by van Hasselt is not easy to locate, it is worth citing the relevant passage here.

Macrura is first mentioned in a letter from van Hasselt to Temminck published in the *Algemeene Konst- en Letter-Bode*, **1**, No. 20, 16th May, 1823, and titled " Uittreksel uit een' Brief van Dr. J. C. van Hasselt aan den Heer C. J. Temminck."

> p. 329 " De Koelee (?) van Russ. Tab. 195 is hier in groote hoeveelheid, en hierbij voegt zich eene, welke ik heb doen afbeelden en den naam *Macrura* gegeven heb "*

The Koelee is the *Keelee* of Russell (1803). No figure accompanies the text (but see below, p. 142). The use of a capital initial letter for *Macrura* does not necessarily indicate a generic name, since capitals are occasionally, and for no apparent reason, used elsewhere in the text (*Clupea Melostoma* for example). A translation of this letter, published the following year (1824) in the *Bull. Sci. nat. geol.* (*Ferussac*), **2** : 89–92, confirms that *Macrura* was intended as a specific name.

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*" The Koelee (?) of Russ. Plate 195 is here in large numbers, and to that must be added one which I have had figured and have given the name *Macrura*."

p.92 " Dans le genre *Clupea* Lin. mes collections sont plus riches ; j'ai divers individus du *Cl. melastoma* Schn., et l'espèce representée par Russell, pl. 195, se trouve ici en quantité ; il faut y joindre une autre espèce que j'ai fait dessiner sous le nom de *macrura*."

Macrura van Hasselt should not, therefore, appear in the synonymy of *Hilsa*.

Subgenus ***Hilsa***

As defined in key. A single species recognised here, *H.* (*Hilsa*) *kelee.*

Hilsa kelee (Cuvier)

Clupea kelee Cuvier, 1829, *Règne animal*, ed. 2, **2** : 320 (on *Keelee* Russell, 1803, *Fishes of Coromandel*, **2** : 75, pl. 195 upper figure : type locality, Vizagapatam).

Macrura kelee : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 627 ; Smith, 1949, *Sea Fishes S. Africa* : 90 ; Munro, 1955, *Mar. F-water fish. Ceylon :* 24 ; Fowler, 1956, *Fishes of the Red Sea :* 69 ; Fourmanoir, 1957, *Mem. Inst. Sci. Madagasc. Serv. océanogr.*, **1** : 8, fig. 1.

?*Clupeonia blochii* Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 353 (type locality, Tranquebar).

Hilsa blochii : Fowler, 1926, *J. Bombay nat. Hist. Soc.*, **30** (4) : 3 ; *Idem*, 1938, *List. Fish. Malaya* : 27.

Alosa brevis Bleeker, 1848, *J. Ind. Arch.*, **2** : 638 (type locality, Bima, Sumbawa Island) ; *Idem*, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 116.

Hilsa brevis : Fowler, 1928, *Mem. Bishop Mus.*, **10** : 30.

Macrura brevis : Munro, 1958, *Papua New Guinea agric. J.*, **10** (4) : 116.

Alausa kanagurta Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 13, 34 (type locality, Batavia, Muntok, East Indies) ; *Idem*, 1865, *Ned. Tijdschr. Dierk.*, **2** : 35, 176.

Alosa kanagurta : Bleeker, 1872, *Atlas Ichth. Ind. Neérland.*, **6** : 114, pl. 265, fig. 5 ; Bean & Weed, 1912, *Proc. U.S. nat. Mus.*, **42** : 590 ; Hora, 1924, *Mem. Asiatic Soc. Bengal*, **6** : 480 ; Suvatti, 1937, *Index Fish. Siam* : 9.

Clupea kanagurta : Day, 1878, *Fishes of India*, pt. 4 : 640, pl. 162, fig. 4 ; *Idem*, 1889, *Fauna British India, Fishes*, **1** : 377 ; Pillay, 1929, *J. Bombay nat. Hist. Soc.*, **32** (2) : 355 ; Tirant, 1929, *Serv. océanogr. Pêches Indochine*, 6ᵉ note : 118, 120 ; Hardenberg, 1931, *Treubia*, **13** (1) : 111.

Clupea (*Alosa*) *kanagurta :* Weber & de Beaufort, 1913, *Fishes Indo-Aust. Archipelago*, **2** : 67 ; Chabanaud, 1926, *Serv. océanogr. Pêches Indo-Chine*, 1ᵉ note : 8.

Hilsa kanagurta : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 304 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **86** : 86 ; *Idem, op. cit.*, **87** : 90, fig. 8 ; Suvatti, 1937, *Index Fish. Siam* : 12 ; Fowler, 1938, *List Fish. Malaya* : 27 ; Bertin, 1940, *Bull. Mus. Hist. nat. Paris*, (2) **12** : 281 (Bleeker cotype) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 63 ; Misra, 1947, *Rec. Ind. Mus.*, **45** (4) : 390 ; Quereshi, 1957, *Agric. Pakistan*, **8** (2) : 107.

Hilsa ganagurta : Chu, 1931, *Biol. Bull. St. John's Univ.*, **1** : 14 (misspelt).

Harengula kanagurta : Paradice & Whitley, 1927, *Mem. Queensland Mus.*, **9** : 76, pl. 12, fig. 1 ; McCulloch, 1929, *Aust. Mus. Mem.*, **5** : 39 ; ?Wu, 1929, *Contr. Biol. Lab. Sci. Soc. China*, **5** (4) : 17, fig. 13 (see note on distribution, below).

Alausa ilisha : (*non* Hamilton-Buchanan) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 33 ; Kner, 1865, *Reise Novarra, Fische* : 331.

Clupea ilisha : Günther (*part*), 1868, *Cat. Fish. Brit. Mus.*, **7** : 445 ; Day (*part*), 1878, *Fishes of India*, pt. 4 : 640 ; *Idem* (*part*), 1889, *Fauna Brit. India*, **1** : 376.

Alausa brachysoma Bleeker, 1853, *Nat. Tijdschr. Ned. Ind.*, **5** : 527 (type locality, Padang, Sumatra) (*non Sardinella brachysoma* Bleeker).

Alosa brachysoma : Bleeker, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 115, pl. 262, fig. 5.

Hilsa brachysoma : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 305.

Alosa chapra : Günther, 1866, *Fishes of Zanzibar* : 123.
Alosa malayana Bleeker, 1866, *Ned. Tijdschr. Dierk.*, **3** : 294 (type locality, Java, Sumatra) ; *Idem*, 1872, *Atlas Ichthy. Ind. Néerland.*, **6** : 114, pl. 265, fig. 4.
Clupea platygaster Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 448 (on Bleeker's Sumatra specimen of *Alausa brachysoma* in British Museum) ; Regan, 1914, *Trans. zool. Soc. London*, **20** (6) : 276.
Clupea (*Alosa*) *platygaster* : Weber & de Beaufort, 1913, *Fishes Indo-Austr. Archipelago*, **2** : 66, fig. 24 ; Chevey, 1932, *Inst. océanogr. Indochine*, 19^{e} note : 9.
Alosa platygaster : Roxas & Martin, 1937, *Dept. Agric. Comm. Manila Tech. Bull.*, **6** : 21 ; Herre, 1953, *List. Philipp. Fishes* : 71.
Clupea durbanensis Regan, 1906, *Ann. Natal Gov. Mus.*, **1** (4) : 4, pl. 4 (type locality, Durban Bay) ; *Idem*, 1908, *op. cit.*, **1** (3) : 242 ; Gilchrist & Thompson, 1908, *Ann. S. Afr. Mus.*, **6** : 268 ; Gilchrist, 1913, *Marine Biol. Rep. S. Africa*, No. 1 : 59.
Paralosa durbanensis : Regan, 1916, *Ann. Durban Mus.*, **1** : 167 ; Gilchrist & Thompson, 1917, *Ann. Durban Mus.*, **1** (4) : 297.
Hilsa durbanensis : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 305 ; Barnard, 1925, *Ann. S. Afr. Mus.*, **21** (1) : 111 ; Fowler, 1925, *Proc. Acad. nat. Sci. Philad.*, **77** : 195 ; Barnard, *Ann. S. Afr. Mus.*, **21** (2) : 1017 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **86** : 411 ; *Idem*, 1935, *op. cit.*, **87** : 365.

Note on synonymy.

Following Regan (1917), many modern authors have either doubtfully cited or ignored *Clupea kelee* Cuvier, 1829 (name without description in footnote, p. 320 in 2nd edition), but Fowler (1941) and Smith (1949) give Cuvier's name priority over *kanagurta* Bleeker. Cuvier states, however, that his *C. kelee* is based on Russell's figure of *Keelee*. Cuvier's name is thus a valid indication, being " a bibliographic reference to a previously published description, definition or figure " (Art. 16 (a), International Code of Zoological Nomenclature 1961).

Günther (1868, p. 445) included *Alausa toli* Cantor in his synonymy of *Clupea ilisha*. The smaller of the two Cantor specimens listed by Günther is *H. kelee* ; the larger is probably *H. toli* (but see p. 135). The remaining specimens listed by Günther under *Clupea ilisha* are *H. kelee.*

Alosa malayana Bleeker, as Weber and de Beaufort (1913) point out, seems to have been based on a juvenile specimen of *H. kelee*. Since eye diameter shows negative allometry with standard length, the maxilla appears to be shorter in smaller fishes, barely reaching to eye centre.

I have followed Fowler (1941) and Day (1878) in placing *Clupeonia blochii* Valenciennes in this synonymy, but have done so tentatively since Valenciennes based his description on the doubtful *Clupea sinensis* Bloch (see notes on the synonymy of *H. toli*).

Fowler (1941) followed Regan (1917) in separating *H. durbanensis* and *H. brachysoma* from *H. kelee*, distinguishing the first by its shorter head, and the second by its deeper body. In Figure 7A and B, head length and body depth are plotted (as percentages of standard length) for the specimens listed under Study Material. The figure shows that there is considerable variation (possibly sexual) in body depth, but that this cannot be ascribed to regional variation. In head length, the Durban specimens (i.e. *H. durbanensis*) have shorter heads than do the Gulf of Aden fishes, but the remaining Indian Ocean specimens are intermediate. On the basis of head length, the Gulf of Aden fishes might be recognised as distinct, but in all other

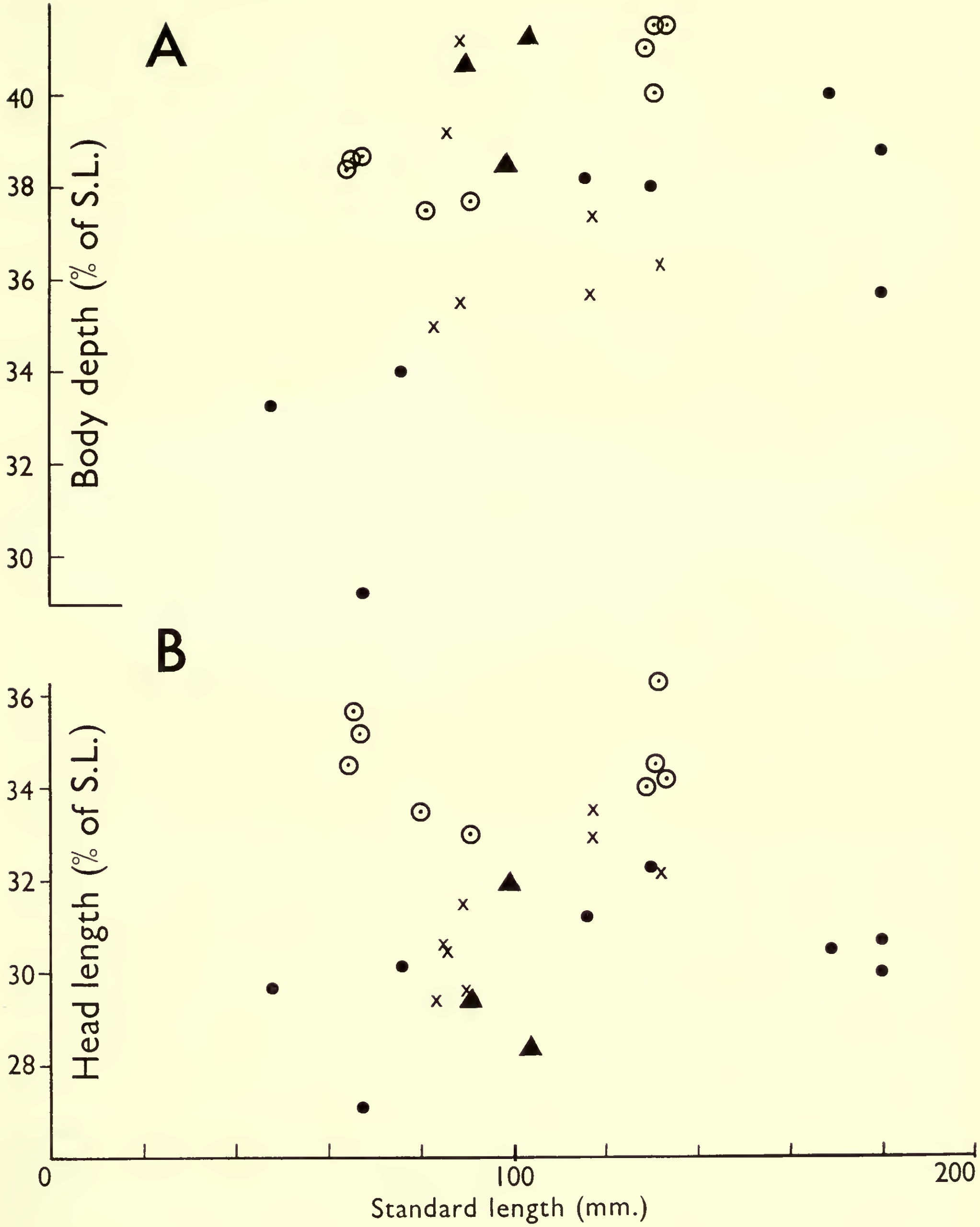

FIG. 7. Body depth (A) and head length (B) as percentages of standard length, plotted against standard length for specimens of *Hilsa kelee*. ● Durban, Kenya coast, Zanzibar. ⊙ Gulf of Aden. x East Indies. ▲ India.

morphometric and meristic measurements they are inseparable from the rest. I have found no other means of distinguishing *H. durbanensis* and *H. brachysoma*, and therefore recognise a single Indo-Pacific member of the subgenus *Hilsa*.

Description. Based on 24 specimens over 50 mm. listed under Study Material. In percentages of standard length : body depth (29·2) 33·3–41·5 (Figure 7A), head length 27·1–36·3 (Figure 7B) ; snout length (5·7) 6·4–8·5 ; eye diameter 7·2–9·5, maxilla length 12·0–16·4 ; operculum, height 15·9–20·6, width 6·9–10·0 ; pectoral length 17·8–21·0, pelvic length 10·3–12·1, anal base 16·7–17·5 ; pre-dorsal 41·7–50·5, pre-pelvic 49·8–57·5.

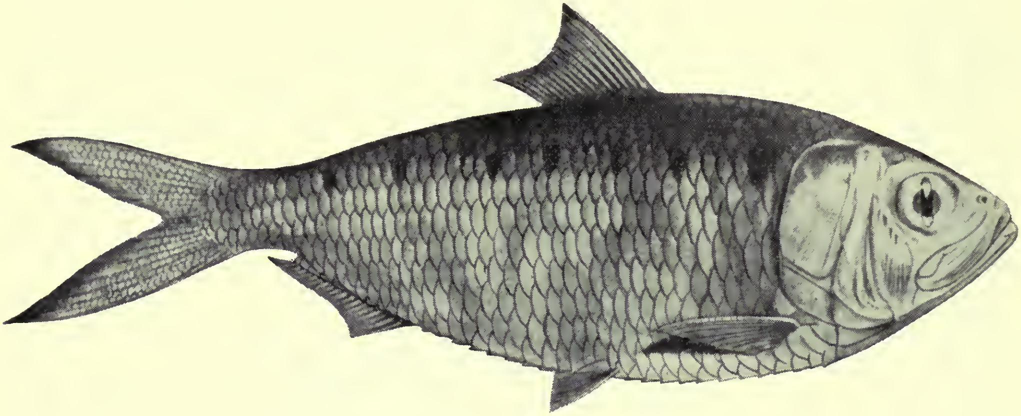

Fig. 8. *Hilsa kelee* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth a little greater than head length. Snout a little smaller than eye diameter, pre-orbital length (i.e. including eye) equal to post-orbital length. Lower jaw included when mouth firmly shut ; maxilla length equals pre-orbital length, extending to below middle or posterior part of eye ; exposed portion with longitudinal ridges ; two supra-maxillae. Pseudobranch shape as in Figure 6B ; a groove present below base of pseudobranch. Dorsal with low scaly sheath ; dorsal origin just nearer to snout tip than to caudal base ; pelvic origin below 3rd–5th branched dorsal rays, usually nearer to caudal base than to snout. Pectorals not reaching pelvic base ; in larger fishes, a groove, to receive upper edge of pectoral ; no axillary pectoral scale. Pelvics about three-fifths of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, about three-quarters length of fin. Anal with low scaly sheath ; anal origin slightly nearer to caudal base than to pelvic base. Caudal fin just longer than head, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over suborbitals, preoperculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil. Dorsal surface of head with thin cutaneous covering, numerous fronto-parietal striae exposed, as shown in Figure 1A.

Cleithral lobe prominent (Figure 3A). Gill filaments of outer hemibranch on first arch about half length of those of the inner hemibranch (Figure 3A). Gillrakers of second to fourth arches curled outwards, about 100 short serrae along inner margin of each raker (Figure 4B) ; gillrakers on lower part of first arch longer than corresponding gill filaments. Opercular bones as in Figure 5A.

Dorsal iv 13–14, pelvic i 7, anal iii 17–19. Pre-pelvic scutes 16 (Regan gives 16–18), post-pelvic scutes 12–13 (Regan 11–13), total 28–30. Scales in lateral series 42–45, 13–14 in transverse series (after Regan). Gillrakers fine and numerous, about 100–150 on lower part of first arch.

COLOUR IN ALCOHOL : Back and upper parts of head brown, flanks silvery. A dark humeral blotch followed (in some specimens) by seven or eight smaller black blotches. Tips of anterior dorsal rays dusky, caudal tips faintly dusky.

DISTRIBUTION: Natal, East African coast, Gulf of Aden, coasts of India, Burma and Siam. The record from Amoy (Wu 1929) was perhaps based on a juvenile of *H. reevesii*, as also a Cambodia record (Chevey and Le Poulain 1940).

SIZE : Up to 220 mm. (Regan).

TYPE MATERIAL : The type of *Hilsa kelee* is Russell's figure of Keelee. Although a poor drawing by modern standards, it is adequate to establish the identity of the species. I have found no reference to any specimens of *H. kelee* on which Russell might have based his drawing. The type of *Alosa brevis* Bleeker was apparently lost shortly after its description (Bleeker 1872). The holotype of *Clupea platygaster* Günther, a syntype of *Alausa kanagurta* Bleeker, and the syntypes of *Clupea durbanensis* were examined and are listed below.

Study Material.

1 fish, 130 mm., purchd. of Mr. Franks (1862.2.4.10).
1 fish, 132 mm., purchd. of Mr. Damon (1866.8.14.100).
1 fish, 98 mm., Bleeker Collection (1867.11.28.25).
5 fishes, 83–117 mm., Madras, coll. F. Day (1889.2.1.1979–83).
1 fish, 117 mm., Orissa, coll. F. Day (1889.2.1.1986).
1 fish, 89 mm., Kurrachee, coll. F. W. Townsend (1898.12.24.59).
1 fish, 48 mm., Sabaki mouth, Kenya (1955.1.18.1).
4 fishes, 129–133 mm., Aden, coll. Fraser-Brunner (1962.3.26.202–205).
5 fishes, 65–91 mm., Jibuti, coll. Fraser-Brunner (1962.3.26.206–210).
1 fish, 103 mm., *Alausa brachysoma* Bleeker HOLOTYPE of *Clupea platygaster* Günther), Padang, Sumatra, purchd. of Dr. Bleeker (1867.11.28.24).
1 fish, 132 mm., SYNTYPE of *Alausa kanagurta* Bleeker, no locality (1867.11.28.26).
1 fish, 90 mm., "*Harengula* (*Paralosa*) *zeylanica*" of Sale Catalogue (1879), Ceylon? (Rijksmuseum, Leiden, No. 7495) (unpublished Bleeker name).
2 fishes, 169 and 180 mm., SYNTYPES of *Clupea durbanensis* Regan, Durban (1905.6.8.19–20).
1 fish, 76 mm., Durban, Natal (1919.4.1.1).
2 fishes, 67 and 180 mm., Durban, Natal (1919.9.12.1–2).

1 fish, 116 mm., Durban, Natal (1915.7.6.2).
(Dry specimens)
1 fish, 102 mm., Pinang (*Alausa toli* from Cantor's collection) (1860.3.19.439).
1 fish, 130 mm., Zanzibar, Playfair Collection (1867.3.9.371).

Subgenus ***Tenualosa***

As defined in the key, p. 127. Four species recognised here.

KEY TO THE SPECIES of *Tenualosa*

I Caudal lobes as long as head ; pseudobranch rather attenuated and with groove below (Figure 6A).

- a Upper (exposed) border of suboperculum contained more than twice in depth of operculum ; scales 45–48 in lateral series ; coasts and rivers from Arabia to Burma . . . . **H. (Tenualosa) ilisha**
- b Upper (exposed) border of suboperculum contained less than twice in depth of operculum ; scales 42–45 in lateral series ; coasts and rivers of China **H. (Tenualosa) reevesii**

II Caudal lobes longer than head ; pseudobranch not attenuated, without ventral groove (Figure 6B).

- a Maxilla short, not reaching eye centre ; suboperculum almost rectangular, its upper (exposed) border almost horizontal ; cleithral lobe small but present **H. (Tenualosa) macrura**
- b Maxilla longer, reaching eye centre or beyond ; suboperculum with rounded posterior margin, upper (exposed) border more steeply inclined, as in Figure 5A ; cleithral lobe barely apparent, as in Figure 3B . . **H. (Tenualosa) toli**

H. macrura, with very long caudal lobes and a short maxilla, is fairly distinctive, but *H. ilisha*, *H. toli* and *H. reevesii* are extremely alike, especially in juvenile stages. In examining stuffed specimens, where the pseudobranch character cannot be checked and where the caudal lobes are often damaged, it is difficult to distinguish between *H. toli* and *H. ilisha*. The difference between these two species in scale counts and in the lengths of the maxilla, head and caudal lobes might perhaps be ascribed to mere geographical variation. But the difference in pseudobranch shape, and the presence or absence of a groove below it, appear to be sufficiently consistent for the two species to be kept separate. *H. reevesii*, on the other hand, may yet prove to be only a subspecies of *H. ilisha* when more specimens are available.

Hilsa ilisha (Ham. Buch.)

Clupanodon ilisha Hamilton-Buchanan, 1822, *Fishes of the Ganges* : 243, 382, pl. 19, fig. 73 (type material from : Ganges estuaries, Patua, Goya Rarra, Calcutta, Dhasa).

Alausa ilisha : Cantor, 1850, *J. Asiatic Soc. Bengal*, **18** : 1282 ; Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 33 ; Kner, 1865, Reise *Novarra*, Fische : 331.

Clupea ilisha : Day, 1878, *Fishes of India*, pt. 4 : 640, pl. 172, fig. 3 ; *Idem*, 1889, *Fauna Brit. India, Fishes*, **1** : 376, fig. 115 ; Lloyd, 1907, *Rec. Ind. Mus.*, **1** : 221 ; Tirant, 1929, *Serv. océanogr. Pêches Indo-Chine*, 6^e note : 118.

Clupea (*Alosa*) *ilisha :* Steindachner, 1896, *Ann. Hofmus. Wien.*, **11** : 228.

Hilsa ilisha : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 306 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 ; Shaw & Shebbeare, 1937, *J. Asiatic Soc. Bengal*, **3** : 13 ; Bertin, 1940, *Bull. Mus. Hist. nat. Paris*, (2) **12** : 281 ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 63, fig. 28 ; Misra, 1947, *Rec. Ind. Mus.*, **45** (4) : 389 ; Pillay, 1952, *Proc. Indo-Pac. Fish. Counc.*, **3** (Section 2 s 2/8) ; Pillay, 1954, *J. Asiatic Soc. Bengal*, **20** (1) : 69 ; *Idem*, 1957, *Indian J. Fish.*, **4** (2) : 345 ; Quereshi, 1957, *Agric. Pakistan*, **8** (2) : 104, fig. 6a ; Khalaf, 1961, *Fishes of Iraq, Baghdad* : 17 ; Mahdi, 1962, *Fishes of Iraq, Baghdad* : 11 ; Pillay & Rosa, 1963, *FAO Fish. Biol. Synopsis* No. 25 : 1, figs. 1 (adult), 3 (embryos), 4–6 larvae and juveniles).

Macrura ilisha : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 633 ; *Idem*, 1956, *Fishes of Red Sea*, **1** : 69.

Tenualosa ilisha : Munro, 1955, *Mar. F-water Fishes Ceylon* : 25.

Clupea palasah Cuvier, 1829, *Règne animal*, ed. 2, **2** : 320 (on *Palasah* Russell, 1803, *Fishes of Coromandel*, **2** : 77, pl. 198 (type locality, Vizagapatam) ; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 445.

Alausa palasah : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 432 (*part*, i.e. Ganges and Malabar specimens only) ; Jerdon, 1849, *Madras J. Lit. Soc.*, **15** : 345 ; Day, 1865, *Fishes of Malabar* : 235.

Clupea (*Alosa*) *palasah :* Steindachner, 1896, *Ann. Hofmus. Wien*, **11** : 229.

Note on synonymy.

The description of *Clupea ilisha* given by Hamilton-Buchanan (1822) must be presumed to refer to this species, even though the figure shows a fish with the short maxilla (not reaching posterior eye border) and a suggestion of the longitudinal ridges on the maxilla characteristic of *H. kelee*. However, the latter species can be excluded since Hamilton-Buchanan emphasises the presence of pectoral axillary scales, which are absent in *H. kelee ;* also, the dorsal view of the head shows no fronto-parietal striae. Hamilton-Buchanan distinguished his species from the *Palasah* of Russell (1803, p. 77, pl. 198) because of a very slight difference in fin-ray counts and because the *Palasah* apparently lacked pelvic axillary scales ; such pelvic axillary scales are, however, present in all species of *Hilsa*. Since Russell also describes a pectoral axillary scale, and since neither Russell nor Hamilton-Buchanan show the long caudal lobes characteristic of *H. toli* and *H. macrura*, it must be presumed that both were referring to the present species. Bleeker (1852) similarly made a distinction between *Palasah* and this species, mainly on pectoral length ; but the pectorals in *H. ilisha* vary in length (in my material), sometimes reaching the pelvic base and sometimes falling far short of this point.

As mentioned earlier, much of the material listed by Günther (1868, p. 446) under *Clupea ilisha* can be referred to *H. kelee*. There is, however, a specimen (skin) from Cantor's collection (225 mm., Ikan Truboh) which may be *H. toli ;* there are only 40 scales in lateral series (*H. ilisha* 45–48) but the (damaged) caudal lobes seem to be too short. Unfortunately the diagnostic pseudobranch character cannot be checked.

Three of the four stuffed specimens listed by Günther (p. 445) under *Clupea palasah* are *H. ilisha ;* one Gangetic specimen is missing.

Of the fishes mentioned by Valenciennes under *Alausa palasah*, two specimens from the Ganges and one from Malabar are *H. ilisha*, but a specimen from Bombay and one from Pondicherry are *H. toli*.

DESCRIPTION. Based on 24 fishes, 99–325 mm. standard length from the coasts of India, and from the Persian Gulf and the River Tigris (see list of study material).

In percentages of standard length : body depth 31·0–39·5, head length 28·6–33·5 ; snout length 5·8–7·3, eye diameter 4·6–6·8, maxilla length 12·2–14·5 ; operculum, height 13·6–15·7, breadth 7·5–9·6 ; pectoral length 18·3–21·5, pelvic length 10·8–12·8, caudal length 25·7–33·2 ; pre-dorsal distance 47·0–52·0, pre-pelvic distance 51·0–55·0. In relation to standard length, eye diameter shows negative allometry, and there is an indication that pectoral and pelvic lengths may show positive allometry.

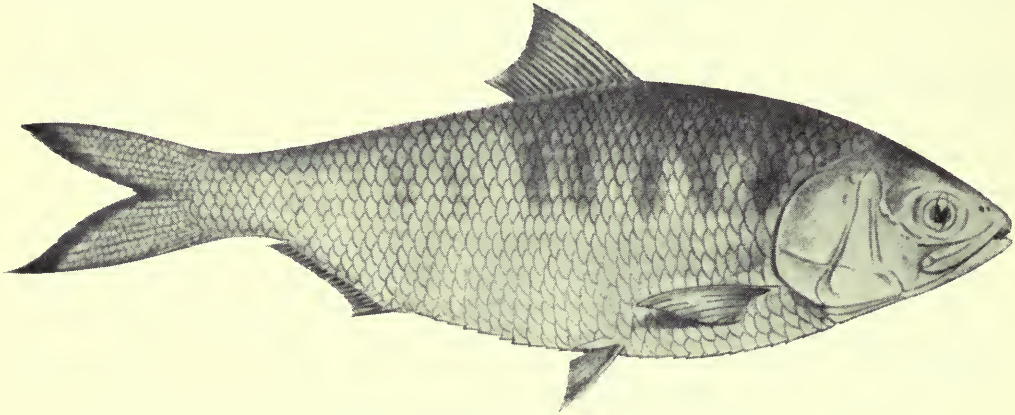

FIG. 9. *Hilsa ilisha* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth variable, a little greater than head length. Snout greater than eye diameter in fishes over about 100 mm., less than eye diameter below this ; pre-orbital length (including eye) two-thirds of post-orbital length. Lower jaw included when mouth firmly shut ; maxilla length just less than pre-orbital length, extending almost to posterior border of eye, exposed portion without longitudinal ridges but occasionally with faint longitudinal striae ; two supra-maxillae. Pseudobranch attenuated, as shown in Figure 6A ; a groove present below border of pseudobranch. Dorsal with low scaly sheath ; dorsal origin just nearer snout tip than base of caudal ; pelvic origin below 1st–4th branched dorsal rays, just nearer to caudal base than to snout. Pectorals variable, sometimes reaching pelvic base ; axillary scale present, half length of pectoral. Pelvic fins about three-fifths length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, about half length of fin. Anal with scaly sheath ; anal origin equidistant between pelvic base and caudal base ; anal longer than in *H. reevesii*, its base greater than distance snout tip to anterior margin of pre-operculum. Caudal fin equal to or just shorter than head length, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over suborbitals, pre-operculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil.

Dorsal surface of head thickly covered by skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges through skin (see Figure 1B). Cleithral lobe not prominent, barely interrupting cleithral outline (Figure 3B). Gill filaments of outer hemibranch on first arch half to three-quarters length of those of inner hemibranch (Figure 3B). Gillrakers on all arches straight or slightly curved, not curled outwards, tips pointed, as long as corresponding gill filaments in adults (Figure 4A). Bones of opercular series resembling those of *H. kelee* (Figure 5A).

Dorsal iv–v 14-16, pelvic i 7, anal ii–iii 18-20, branchiostegal rays 5. Pre-pelvic scutes* (14) 15–19, post pelvic scutes (10) 11–15 (16), total (26) 27–32 (33) (612 fishes). Scales in lateral series (39–44) 45–49 (49) (443 fishes), in transverse series 17–20 ; exposed portion of scales with numerous longitudinal striae, edge of scale pectinated, especially in larger fishes ; minute scales covering caudal, except along posterior border. Gillrakers fine and numerous, 120 (young) to 200 on lower part of first arch (after Regan). Trunk vertebrae 12–13, caudal vertebrae without haemal spines (10) 11–12 (13), caudal vertebrae with haemal spines 20–22 (23), total vertebrae (44) 45–46 (114 fishes).

The regressions of various body measurements on standard length for Hooghly river and Chilka Lake specimens were calculated by Pillay (1957), who showed significant differences between samples from these two localities in five non-meristic characters. Pillay and Rosa (1963), summarising earlier studies, stated that " each major river system, the Chilka Lake and the Saurashtra Coast have their own stocks of *hilsa* and there is very little, if any, intermingling among them". The differences between these stocks involve meristic as well as non-meristic characters, and in addition, fishermen report differences in taste (dependent probably on fat content).

The skull of *H. ilisha* has been described and figured by Moona (1959), the pharyngeal pockets by Kapoor (1955), the swim-bladder by Srivastava (1955), blood characteristics by Pillay (1954, 1958), and the branchial skeleton by Khanna (1961).

Colour : " Silvery, shot with gold and purple ; no spots in the adult, but a row of them along the upper third of the body in the immature " (Pillay & Rosa) ; in alcohol, body brown, sometimes still silvery, upper surfaces darker, fins hyaline.

Bionomics, fishery, etc. :

H. ilisha has considerable economic importance in Indian waters (especially in the Bay of Bengal) and in Pakistan and Burma. Following a symposium in 1952, current information on the *Hilsa* fisheries was assembled (*J. Asiatic Soc.*, **20** (1) : 1–79 (1954)) by the Hilsa Sub-Committee of the Indo-Pacific Fisheries Council. The many papers dealing with the bionomics, life history and fishery of *H. ilisha* published since then have been usefully summarised by Pillay and Rosa (1963).

The esteem in which the ' hilsa ' is held in Bengal is reflected in the many references to its quality and flavour in Sanskrit and Bengali literature,* while Day (1878) and other writers testify to the popularity of the 'sable fish' amongst Europeans.

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*Scute, scale and vertebral counts are from Hooghly river and Chilka Lake specimens examined by Pillay (1957) ; rare counts placed in parenthesis. My material lies well within these ranges.

SIZE: Females attain a larger size than males (Pillay & Rosa, 1963). On the Godavari, Chacko and Ganapati (1949) recorded females of 356–600 mm., and males of 300–432 mm. On the same river, Pillay and Rao (in Pillay & Rosa, 1963) record the smallest mature male as 256 mm., and the smallest mature female 370 mm., but in the Hooghly such mature fishes were smaller (160–170 mm. and 190–200 mm. respectively—see Pillay, 1958).

DISTRIBUTION: Persian Gulf (Tigris, Euphrates, Lake Hammar), West Pakistan (Indus), west coast of India, Ceylon, Bay of Bengal, deltaic area of Burma, coastal waters of Cochin China (see Pillay and Rosa, 1963).

TYPE MATERIAL: The type of *Hilsa ilisha* is Hamilton-Buchanan's figure (Pl. 19, fig. 73). It was based on a juvenile, which might account for the rather short maxilla. But the anal branched ray count (19) distinguishes it from *H. toli*, as also does the short caudal. The absence of fronto-parietal striae, and the presence of a pectoral axillary scale rule out *H. kelee*. Paratypes of *Alausa palasah* are listed below.

Study material.

3 fishes, 115–131 mm., Tigris (1875.1.14.11–13).
2 fishes, 208–290 mm., Calcutta (1889.2.1.1962-3).
9 fishes, 30–115 mm., Orissa (1889.2.1.1964–9) + (3 unregistered).
7 fishes, 52–101 mm., Madras (1889.2.1.1970–5) + (1 unregistered).
1 fish, 212 mm., Canara (1889.2.1.1976).
3 fishes, 68–79 mm., Sind (1889.2.1.1977–8) + (1 unregistered).
1 fish, 323 mm., Bombay (1889.2.1.2022).
6 fishes, 97–146 mm., Sittang R. (1891.11.30.396–401).
2 fishes, 297–323 mm., Ganges, PARATYPES of *Alausa palasah* Valenciennes (M.N.H.N.Paris No. 3685–6)
1 fish, 195 mm., Malabar, coll. Dussumier (M.N.H.N.Paris 4976).
1 fish, 325 mm., Ormara, Meknam Coast (1899.5.8.11).
6 fishes, 99–127 mm., Basra (1920.3.3.178–82) + (1 unregistered).
25 fishes, 63–135 mm., Padma R., Bengal (1923.6.30.1–10) + (15 unregistered).
1 fish, 108 mm., Bengal (1934.10.17.11).
(Dry specimens)
1 fish, 350 mm., R. Tigris (1875.1.14.14).
1 fish, 360 mm., R. Tigris (1875.1.14.15).
†1 fish, 370 mm., India (1861.4.2.2).
1 fish, 410 mm., Madras (1883.11.26.81).
†1 fish, 340 mm., Suttapore, Ganges (1848.2.1.66).
†1 fish, 300 mm., Suttapore, Ganges (1848.2.1.65).

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*For example, hilsa is described as *matsyaraja* (king of fishes), and elsewhere it is said, *Illisah jitapiyusah* (Hilsa surpasses nectar)—see Hora 1954.

†*Clupea palasah* of Günther (Catalogue, p. 445).

Hilsa reevesii (Richardson)

Alosa reevesii Richardson, 1846, *Ichthy. China Japan* : 305 (type locality, China seas).

Alausa reevesii : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 437 ; Sauvage, 1881, *Bull. Soc. Philom. Paris* (ser. 7) **5** : 107.

Clupea reevesii : Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 446 ; Peters, 1880, *Monatsh. Akad. Wiss. Berlin* : 926 ; Günther, 1889, *Ann. Mag. nat. Hist.* (ser. 6) **4** : (219) 229 ; Elera, 1895, *Cat. Fauna Filip.*, **1** : 583 ; Rutter, 1897, *Proc. Acad. nat. Sci. Philad.*: 64.

Hilsa reevesii : Regan, 1917, *Ann. Mag. nat. Hist.*, (ser. 8) **19** : 306 ; Chu, 1931, *Biol. Bull. St. John's Univ.*, No. 1 : 13 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 ; Kimura, 1935, *J. Shanghai Sci. Inst.*, (sect. 3) **3** : 104 ; Mori, 1952, *Mem. Hyogo Univ. Ag.*, **1** (3) : 32.

Macrura reevesii : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 630.

Alausa palasah : (*non* Cuvier) Richardson, 1846, *Ichthy. China Japan* : 306 ; Cantor, 1849, *J. Asiatic Soc. Bengal*, **18** : 282 (based on Richardson's specimen).

?Harengula kanagurta : Wu, 1929, *Contr. Biol. Lab. Sci. Soc. China*, **5** (4) : 17, fig. 13.

?Clupea (*Alosa*) *thibaudeani :* Durand, 1940, *Notes Inst. océanogr. Indochine*, **36** : 6, fig. 1 ; Chevey & Le Poulain, 1940, *Trav. Inst. océanogr. Indochine*, 5^{e} mem.: 19.

?Clupea (*Alosa*) *kanagurta :* Chevey & Le Poulain, 1940, *Trav. Inst. océanogr. Indochine*, 5^{e} mem.: 19.

Note on synonymy.

Fowler (1941, p. 630) included *Clupea palasah* Günther in this synonymy, but as noted earlier, three of Günther's four specimens are *H. ilisha* and the fourth is missing.

Durand (1940) compared his *Clupea* (*Alosa*) *thibaudeani* with *H. kanagurta*, stating that his fishes had a broader operculum and more gillrakers (operculum breadth 1·5 in height, gillrakers 290). But Durand's figure shows a well-defined pectoral axillary scale, an upper suboperculum border rising very steeply and there is enough detail on the dorsal part of the head to suggest that fronto-parietal striae were absent. It seems likely that Durand's specimens belong to *Tenualosa*, and the high gillraker count, low scale count (40–42) and low dorsal ray count (17) point to *H. reevesii* ; the broad operculum seems to confirm this. A series of black spots are shown on the flanks, but his specimens were 122–240 mm. and were probably juveniles.

The two references to *kanagurta* in the synonymy (from Amoy and Cambodia) are tentatively placed here, mainly on geographical grounds.

DESCRIPTION. Based on five fishes 150–500 mm. standard length from Hong Kong and China (see list of Study Material). Measurements as in *H. ilisha*.

In percentages of standard length : body depth 28·8–33·9, head length 27·4–31·7 ; snout length 6·8–7·5, eye diameter 3·6–6·5, maxilla length 11·2–13·3 ; operculum, height 12·2–15·0, breadth 8·2–9·5 ; pectoral length 18·0–18·8, pelvic length 9·6–11·5, caudal length 28·0–31·2 ; pre-dorsal distance 49·6–50·7, pre-pelvic distance 50·0–51·7. In relation to standard length, eye diameter shows strong negative allometry ; negative allometry may occur also in body depth and snout length in fishes up to 150 mm. in length.

Body strongly compressed, its depth a little greater than head length. Snout greater than eye diameter in fishes over about 150 mm. ; less than eye below this ; pre-orbital length (including eye) about two-thirds of post-orbital length. Lower jaw included when mouth firmly shut ; maxilla length just equal to pre-orbital length, extending just to posterior border of eye, exposed portion without longitudinal ridges but with many fine longitudinal striae in large fishes ; two supramaxillae. Pseudobranch attenuated, as in Figure 6A ; a groove present below lower border of pseudobranch, more pronounced in larger fishes. Dorsal with low scaly sheath ; dorsal origin about equidistant between snout tip and base of caudal ; pelvic origin below anterior unbranched dorsal rays, equidistant between snout tip and caudal base. Pectorals not reaching pelvic base ; axillary scale present, two-fifths length of pectoral. Pelvic fins half length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, just less than half length of fin. Anal with scaly sheath ; anal origin equidistant between pelvic tips and caudal base ; anal base shorter than in *H. ilisha*, less than distance from snout tip to anterior margin of pre-operculum. Caudal fin a little longer than head length, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over sub-orbitals, pre-operculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing whole pupil.

Dorsal surface of head thickly covered by skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges through skin (see Figure 1B). Cleithral lobe not prominent, scarcely breaking cleithral outline (Figure 3B). Gill filaments of outer hemibranch on first arch half to three-quarters length of those of inner hemibranch (Figure 3B). Gillrakers on all arches straight or slightly curved, not curled outwards, tips pointed, as long as or slightly shorter than corresponding gill filaments. Bones of opercular series resembling those of *H. ilisha* but operculum broader, suboperculum longer, and junction between two rising more steeply ; upper (exposed) border of suboperculum less than twice in height of operculum.

Dorsal iv 13–15, pelvic i 7, anal iii 15–17. Branchiostegal rays 5. Pre-pelvic scutes 17*, post-pelvic 14–15, total 31–32. Scales in lateral series 40 (Fowler) 42–45, in transverse series 16–17 (Regan) ; exposed portion of scales with numerous longitudinal striae, edge of scale pectinated in larger fishes ; minute scales on caudal, except along posterior border. Gillrakers fine and numerous, 150 (young) to 250 on lower part of first arch (after Regan).

COLOUR : In alcohol, upper surfaces brown, flanks silvery or golden, no spots on upper part of flank in larger fishes, but a faint series in a specimen of 65 mm. " *Extrémité des pectorals largement rembrunie* (*en eau formolée*) " (Chabanaud 1936).

SIZE : Up to 575 mm. standard length.

DISTRIBUTION : China Seas, Shanghai, Kiukiang, Hong Kong ; Philippines (Elera's records) ; Korea (Fusan) rare (Mori 1952) ; Cambodia (Durand 1940).

TYPE : A mounted skin, as listed under Study Material.

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*Regan (1917) records 18 + 13–14 for the same material, evidently counting as a pre-pelvic scute the small scute between the bases of the pelvics.

Relationship to H. ilisha.

H. reevesii and *H. ilisha* are evidently closely related, the former replacing the latter along the coasts of China. On the basis of my (admittedly meagre) material I am keeping the two separate since further small differences besides that of operculum shape have emerged from analysis of available data.

In *H. reevesii* the pelvic fins are set slightly nearer the snout and, possibly as a result, the anal origin is equidistant between the pelvic *tips* and the caudal base, (pelvic *base* and caudal base in *H. ilisha*). In addition, the anal has slightly fewer branched rays in *H. reevesii* (15–17 ; *cf* 18–20) and the base of the anal is noticably shorter. Thus, in *H. ilisha*, the anal base is almost as long or longer than the pectorals and equal or greater than the distance snout tip to anterior pre-operculum margin ; in *H. reevesii*, the anal base is about two-thirds pectoral length and, measured from snout tip, reaches the posterior border of the eye (juveniles) or a little beyond (adults).

I have included Elera's Philippine records, although these do not appear to have been validated since. If the records of *H. ilisha* from Cochin China are correct, then the Indo-Malayan Archipelago is not the boundary between these two species.

Study Material.

1 fish, 445 mm., China (1934.3.5.1).
1 fish, 365 mm., China (1884.2.26.75).
1 fish, 500 mm., Shanghai (1895.5.31.24)
1 fish, 65 mm., Amoy, China (1928.6.22.1).
1 fish, 234 mm., Hong Kong (1939.3.23.4).
1 fish, 150 mm., China (coll. Reeves) (1963.8.20.1).
2 fishes, 570–575 mm., Kiu Kiang (1888.3.23.44–45).
(Dry specimens)
1 fish, 295 mm., HOLOTYPE of *Clupea reevesii*, China (coll. Reeves) (1963.8.20.2).
1 fish, 140 mm., China (coll. Reeves) (1963.8.20.3).

Hilsa macrura (Bleeker)

Alausa macrurus Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 31 (on *macrura* Kuhl & van Hasselt 1823) (type locality, Batavia, Java).

Alosa macrurus : Bleeker, 1861, *Versl. Meded. Akad. Wet. Amsterdam*, **12** : 64 ; *Idem*, 1868, *op. cit.*, (ser. 2) **2** : 294 ; *Idem*, 1872, *Atlas Ichth. Ind. Néerland*, **6** : 113, pl. 264, fig. 4.

Clupea macrura (Kuhl & van Hasselt) : Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 31 (name in synonymy) ; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 448 ; Vinciguerra, 1926, *Ann. Mus. Civ. Stor. nat. Genoa* (ser. 3) **10** : 619 ; Tirant, 1929, *Serv. océanogr. Pêches Indo-Chine*, 6^e^ note : 119, 174 ; Hardenberg, 1931, *Treubia*, **13** (1) : 111.

Clupea (*Alosa*) *macrura :* Weber & de Beaufort, 1913, *Fish. Indo-Aust. Arch.*, **2** : 65 ; Chevey, 1932, *Inst. océanogr. Indo-Chine*, 19^e^ note : 9.

Hilsa macrura : Regan, 1917, *Ann. Mag. nat. Hist.* (ser. 8) **19** : 307 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 ; *Idem*, 1938, *List Fish. Malaya* : 27.

Macrura macrura : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 632.

Note on synonymy.

As noted below (p. 145), Bleeker's original description of *Alausa macrurus* was based entirely on a figure prepared by Kuhl and van Hasselt, stated by Bleeker to be 310 mm. (Kuhl and van Hasselt are known to have made their drawings life-size wherever possible). A Kuhl and van Hasselt specimen of 420 mm. in the Leiden Museum is thus too large to have been the fish from which the drawing was made. Dr. Boesman informs me (*in litt.*) that this fish is labelled " *Clupea macrura* ", but that there is also a second (old) label " *Clup. palasah* Cuv.". He considers the specimen to be *Hilsa toli* and makes the suggestion that from this specimen a second drawing of *Clupea macrura* may have been made by Kuhl and van Hasselt, and that it was this second drawing that Valenciennes saw and identified (correctly) as *toli*. Whatever the truth in this, it seems certain that no Kuhl and van Hasselt specimen of *Hilsa macrura* exists, and that Bleeker should be accorded authorship of this name.

The type of *Alausa macrurus* Bleeker 1852 is not the Kuhl and van Hasselt drawing on which Bleeker based his description, because this figure was never published (a further reason for considering Bleeker the true author of this name). It is therefore necessary to select a neotype from amongst Bleeker's material.

Bleeker (1853, p. 502) records his first specimen from Batavia, a fish of 342 mm. total length. This fish can be identified with a specimen in the Bleeker collection at the Leiden museum (the larger of two, RMNH 7112) which is 245 mm. standard length and 337 + mm. total length (caudal tips damaged). This specimen is here designated neotype. Dr. Boesman has examined this fish and confirmed its identity for me. The specimen from Bleeker's collection supposed by Günther (1868, p. 448) to be the type of *Clupea macrura* appears to be lost. Bertin (1940) listed a supposed cotype of *Alausa macrurus* Bleeker in the Paris Museum. This fish is *Hilsa macrura* but probably derives from a later collection by Bleeker than that from which the neotype has been selected.

DESCRIPTION. Based on 2 fishes, 141 and 151 mm. standard length from Sarawak; and one fish 181 mm., a Bleeker specimen (see list of Study Material).

In percentages of standard length : body depth (33·7) 37·7–38·0, head length 24·0–25·4 ; snout length 4·9–5·4, eye diameter 5·5–5·8, maxilla length 8·1–8·8 ; operculum, height 11·4–12·9, breadth 5·8–6·4 ; pectoral length 19·9, pelvic length 9·9–11·5, caudal length 46·3–46·5 ; pre-dorsal distance 46·5–48·8, pre-pelvic distance 49·7–51·3. Regan (1917) implies that caudal lobes show positive allometry in relation to head length.

Body strongly compressed, head length about two-thirds of body depth. Snout less than eye diameter ; pre-orbital length (including eye) almost equal to post-orbital length. Lower jaw included when mouth firmly shut ; maxilla length three-quarters of pre-orbital length, reaching to eye centre ; exposed portion smooth, without longitudinal ridges or striae ; two supra-maxillae. Dorsal with low scaly sheath ; dorsal origin a little nearer to snout tip than to base of caudal ; pelvic origin below 3rd–4th branched dorsal rays, equidistant between snout tip and caudal base. Pectorals not reaching pelvic base ; axillary scale present, almost three-quarter pectoral length. Pelvic fins about half length of pectorals, a little nearer to pectoral base than to anal origin ; axillary scale present, three-quarters length of fin. Anal with low scaly sheath ; anal origin equidistant between pelvic base and caudal base. Caudal fin almost twice head length, lower lobe a little longer than upper.

No teeth. Cutaneous sensory canals of head branching over suborbitals, preoperculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing whole pupil.

Dorsal surface of head covered with thick skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges visible through skin. Cleithral lobe intermediate between that of *H. kelee* and *H. ilisha*, to some extent interrupting cleithral outline. Gill filaments of outer hemibranch of first arch three-quarter length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, with a small distal knob (Figure 4C), half length of corresponding gill filaments. Operculum bones as in *H. kelee* but suboperculum more rectangular, and the line of its (exposed) border with the operculum nearer the horizontal (if projected, cutting the dorsal profile far behind the dorsal fin).

Dorsal iv–v 15, pelvic i 7, anal iii 17, branchiostegal rays 5. Pre-pelvic scutes 17 (Regan 16–18, but see footnote p. 140), post-pelvic 14, total 31. Scales in lateral series 45, in transverse series 14–15 (Regan) ; minute longitudinal striae along posterior border of scale ; minute scales covering caudal lobes except along posterior border. Gillrakers fine and numerous, 60–80 on lower part of anterior arch (Regan).

COLOUR : In alcohol, dorsal surfaces brown, flanks silvery or golden, a faint dark humeral spot visible ; fins colourless except for faint dark edge to caudal.

SIZE : 350 mm. (Regan).

DISTRIBUTION : Java, Sumatra, Bankalis, Borneo, Singapore (Weber and de Beaufort, 1913). According to the latter authors " it forms the object of a very important fishery at the mouth of some rivers in Borneo, Malacca and Sumatra ".

TYPE : Neotype, a fish 245 mm. standard length (total length *ca* 337 mm., but caudal tips damaged), Reg. No. RMNH 7112, in the Bleeker collection at the Rijksmuseum van Natuurlijke Historie, Leiden, identified as Bleeker's first specimen from Batavia (see above, p. 142).

Study Material.

1 fish, 151 mm., Sarawak (1868.6.9.2).
1 fish, 141 mm., Sarawak (1895.2.28.72).
1 fish, 181 mm., East Indies, coll. Bleeker (M.N.H.N.Paris No. 2039).

Regan (1917) records a specimen of 350 mm. but I have been unable to find this fish.

Hilsa toli (Valenciennes)

Alausa toli Valenciennes,* 1847, *Hist. Nat. Poiss.*, **20** : 435 (type locality, Coromandel, Pondicherry) ; Cantor, 1849, *J. Asiatic Soc. Bengal*, **18** : 1281.

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*Following Bailey (1951) I have throughout cited Valenciennes as sole author of volume 20 of the Histoire Naturelle des Poissons, 1847.

Alosa toli : Bleeker, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 113, pl. 265, fig. 4.

Clupea toli : Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 447 ; Day, 1878, *Fishes of India*, pt. 4 : 641 ; *Idem*, 1889, *Fauna of Brit. India*, **1** : 377 ; Duncker, 1904, *Mitt. Naturhist. Mus. Hamburg*, **21** : 186 ; Pillay, 1929, *J. Bombay nat. Hist. Soc.*, **33** : 355; Tirant, 1929, *Serv. océanogr. Pêches Indo-Chine*, 6^{e} note : 119 ; Hardenberg, 1931, *Treubia*, **13** (1) : 110 ; *Idem, op. cit.*, **15** (3) : 231.

Clupea (*Alausa*) *toli* : Martens, 1876, *Preuss. Exped. Ost-Asien*, **1** : 405.

Clupea (*Alosa*) *toli* : Weber & de Beaufort, 1913, *Fishes Indo-Aust. Arch.*, **2** : 64 ; Chevy, 1932 (Aug. 25th), *Inst. océanogr. Indo-Chine*, 19^{e} note : 9.

Sardinella toli : Jordan & Evermann, 1902, *Proc. U.S. nat. Mus.*, **25** : 166 ; Jordan & Richardson, 1909, *Mem. Carnegie Mus.*, **4** : 166.

Hilsa toli : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 306; Hora, 1923, *J. nat. Hist. Soc. Siam*, **6** : 174 ; Chu, 1931, *Biol. Bull. St. John's Univ.*, No. 1 : 14 ; Herre & Myers, 1937, *Raffles Mus. Bull.*, No. 13 : 12 ; Smith, 1945, *Bull. U.S. nat. Mus.*, No. 188 : 44 ; Misra, 1947, *Rec. Ind. Mus.*, **45** (4) : 390 ; Quereshi, 1957, *Agric. Pakistan*, **8** (2) : 104, fig. 7.

Alausa palasah : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 432 (*part*, i.e. Bombay and Pondicherry specimens).

?*Clupea macroura* (Kuhl & van Hasselt) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 437 (name only ; misspelt).

Alausa argyrochloris Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 440 (type locality : Ile de France) (the single Dussumier specimen, not the two Quoy & Gaimard specimens—see below).

Alausa ctenolepis Bleeker, 1852, *Natuurk. Tijdschr. Ned. Ind.*, **3** : 74 (type locality, Batavia, Muntok, Singapore).

Clupea chapra : (*non* Ham.-Buch.), Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 447 ; Beavan 1877, *F-water Fish. India* : 118.

Alosa ilisha : (*non* Ham.-Buch.), Bleeker, 1874, *Ned. Tijdschr. Dierk.*, **4** : 148.

?*Clupea ilisha* : Günther (*part*), 1868, *Cat. Fish. Brit. Mus.*, **7** : 445.

Hilsa sinensis : Fowler, 1930, *Proc. Acad. nat. sci. Philad.* (1929) : 592, 598 ; *Idem*, 1938, *List Fish. Malaya* : 28.

Tenualosa sinensis : Munro, 1955, *Mar. F-water Fishes Ceylon* : 24.

Macrura sinensis : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 631 ; Chu & Tsai, 1958, *Quart. J. Taiwan Mus.*, **2** (1–2) : 104.

Note on synonymy.

Fowler (1930) identified this species with *Clupea sinensis* Bloch 1795 and later (Fowler 1941) included it in the synonymy of *Clupea sinensis* Linnaeus. But Linnaeus' description of *C. sinensis*, which appears for the first time in the tenth edition of the Systema Naturae, is too vague for a positive identification to be made (Valenciennes (1847) comments on this and concludes that *Clupea sinensis* Linnaeus, together with *Clupanodon sinensis* Lacepède " doit etre rayé de nos catalogues ichthyologiques "). Of possible Chinese clupeids with moderate anal fins (i.e. about 16 rays) the gizzard shads can be eliminated since a filamentous last dorsal ray is not mentioned ; the dussumieriids *Dussumieria* and *Etrumeus* have too many branchiostegal rays (6 in *C. sinensis*) and *Spratelloides* has too few anal rays (16 in *C. sinensis*) ; *Sardinops* and *Clupea* are possible, but Linnaeus states that *C. sinensis* is similar to *Clupea harengus* " sed latior ".

Daubentòn (1787, p. 202) translates this as " sa largeur est plus considérable ". It is the possibility that depth rather than overall size was meant which prevents exclusion of either *Sardinella* or *Herklotsichthys* from consideration.

Herklotsichthys (*Harengula* auct.) and *Sardinella* are possible since both have the appearance of truncated posterior branchiostegal rays, a character stressed in Linnaeus' description. In both *Herklotsichthys* and *Sardinella*, certain species or individuals either lack, or have feebly developed teeth ("os edentulum" in *C. sinensis*). On the other hand, neither *Herklotsichthys* nor *Sardinella* attain the size of *Hilsa*. Within *Hilsa* itself, *H. reevesii* is also a possibility. But since *Clupea sinensis* does not appear amongst the Linnaean type specimens at Uppsala University listed by Lönnberg (1896) and in view of the inadequacy of the original description I have here preferred to use Valenciennes' name *toli*.

C. sinensis L. of Bloch (1795) does not help to identify Linnaeus' fish. Bloch's figure shows a fish with a black mark at the base of the anterior dorsal rays, which is characteristic of some species of *Sardinella*. There is also a black border to the dorsal and the caudal, such as is found for example in *S. melanura* or *S. sindensis*. Valenciennes (*loc. cit.*) doubted Bloch's identification, believed Bloch's fish to have been different from Linnaeus', and called it *Clupeonia blochii* [placed by Day (1878) and Fowler (1941) in the synonymy of *H. kanagurta* (i.e. *H. kelee*]. Day (*loc. cit.*), however, quotes Prof. Peters (*in. litt.*), who had examined a dried specimen and believed it to be the model for Bloch's figure, stating " I am of (the) opinion *C. sinensis* Bloch is *C. toli*, Cuv. and Val.". Peters also examined this specimen for Günther, who considered it identical to Hamilton-Buchanan's *Clupanodon ilisha* (Günther, 1868, p. 446). Unfortunately, most of Günther's ' *ilisha* ' material is clearly *H. kanagurta* (see p. 130). I do not know whether this specimen is still extant, but the shortness of the maxilla and indeed of the whole head in Bloch's figure, as well as the distinctive black marks on the fins, are much more in accord with *Herklotsichthys* or *Sardinella* than with *Hilsa*. It can be noted, however, that Valenciennes (*loc. cit.* p. 436) describes black dorsal and anal borders in his *Alausa toli* (based on Dussumier's notes). The operculum is too narrow for *H. reevesii* and the caudal is too short for *H. toli*.

The *Clupea sinensis* (or Hareng de la Chine) of Bonnaterre (1788), Daubenton (1788), Ray (1788), Gmelin (1789), and Walbaum (1792) were based on Linnaeus' description ; those of Martens (1876) and Schneider (1801) were based on Bloch.

A further problem concerning this synonymy is the identity of Kuhl and van Hasselt's *macrura*, a drawing of which both Valenciennes and Bleeker saw. Valenciennes (1847, p. 437) believed this fish to be his *Alausa toli*. However, Bleeker (1852, p. 32) maintained Kuhl and van Hasselt's name, showing that Valenciennes' *toli* had a longer head. In the Atlas, Bleeker (1872*) definitely separated the two species (on head length, jaw length and scales). Fowler (1941) tentatively placed *Clupea macroura* (K. v.H.) of Valenciennes in his synonymy for *H. toli*, while still accepting Bleeker's *macrura* as distinct. I have followed the same course, for reasons given in more detail under *H. macrura* (p. 142).

The single Dussumier specimen of *Alausa argyrochloris* Valenciennes is *Hilsa toli*, but the two Quoy and Gaimard specimens from Mauritius are *Sardinella*, probably *S. dayi* Regan. Bertin (1940) was therefore wrong to assume the latter to be paratopotypes of *H. toli*. Valenciennes' Bombay and Pondicherry specimens of *Alausa palasah* are also *H. toli*.

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*I have here accepted the Atlas dating as reconstructed by Mees (1962).

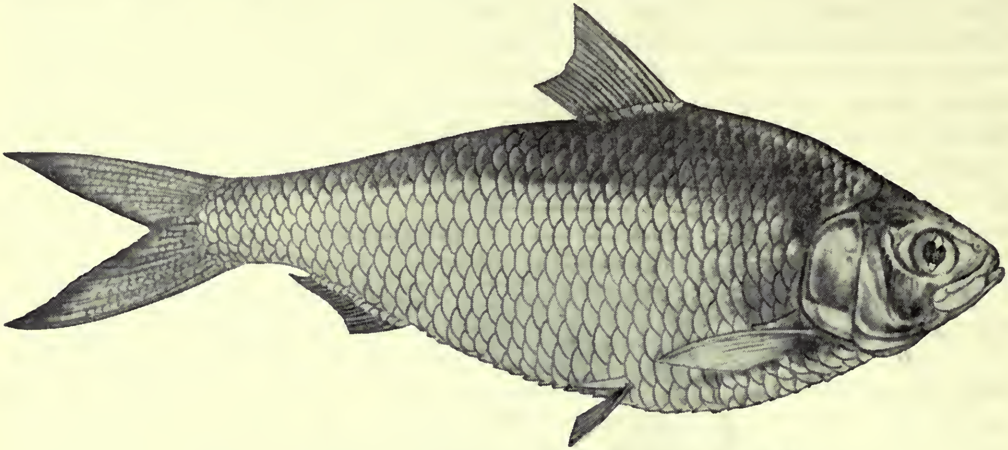

FIG. 10. *Hilsa toli* (from Day, *Fishes of India*, modified).

DESCRIPTION. Based on 11 fishes, 83–396 mm. standard length from the coasts of India and the Indo-Malayan Archipelago (including one of Bleeker's two specimens of *Alausa ctenolepis*, 420 mm. total length—see list of Study Material).

In percentages of standard length : body depth 32·6–39·0, head length 24·8–28·0 ; snout length 5·3–6·5, eye diameter 4·3–7·3, maxilla length 11·2–12·5 ; operculum, height 12·2–14·3, breadth 6·2–7·3 (8·6) ; pectoral length (16·2) 19·2–21·2, pelvic length (9·3) 10·3–13·1, caudal length 33·3–37·6 ; pre-dorsal distance 44·0–49·8, pre-pelvic distance 49·2–54·5. In relation to standard length, eye diameter shows strong negative allometry, and both pectoral and pelvic fins show positive allometry. In these specimens, smaller fishes have slightly deeper bodies.

Body strongly compressed, its depth greater than head length. Snout greater than eye diameter in fishes over about 120 mm., less than eye diameter in juveniles ; pre-orbital length (i.e. including eye) four-fifths of post-orbital length (equal in fishes of 100 mm. or less). Lower jaw included when mouth firmly shut ; maxilla length equal or (in large fishes) greater than pre-orbital length, extending beyond posterior eye border ; exposed portion without longitudinal ridges but occasionally with one or two faint longitudinal striae ; two supra-maxillae. Dorsal with low scaly sheath ; dorsal origin just nearer to snout tip than to caudal base ; pelvic origin below 4th–7th branched dorsal rays, equidistant or just nearer to caudal base than to snout. Pectorals not reaching pelvic base ; axillary scale present, half length of pectoral. Pelvic fins about half length of pectorals, just nearer to pectoral base than to anal origin ; axillary scale present, about two-thirds length of fin. Anal with low scaly sheath ; anal origin just nearer to caudal base than to pelvic base. Caudal fin a little longer than head length, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over sub-orbitals, pre-operculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing all or three-quarters of pupil.

Dorsal surface of head thickly covered by skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges visible through skin. Cleithral lobe not prominent, barely interrupting cleithral outline. Gill filaments of outer hemibranch on first arch half to three-quarters length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, not curled outwards, tips pointed, as long as corresponding gill filaments in adults. Bones of opercular series as in *H. kelee*.

Dorsal iv–v 14–15, pelvic i 7, anal iii 15–17, branchiostegal rays 5. Pre-pelvic scutes 17 (Regan, 17–18), post-pelvic scutes 12–13 (Regan, 11–13), total 29–30. Scales in lateral series about 40, 14–15 in transverse series ; exposed portion of scales with numerous longitudinal striae, edge of scale pectinate, especially in larger fishes ; minute scales covering caudal, except along posterior border. Gillrakers fine and numerous, 70–95 on lower part of first arch (after Regan).

The swim-bladder of *H. toli* has been described by Nayak and Bal (1955), and the food and feeding habits by Chacko (1949).

COLOUR : " Silvery, shot with yellow and purple, a dark shoulder spot in young " (Day, 1878). In preserved material (alcohol), the back is brown, the flanks silver or golden, and the shoulder spot is very faint in the smaller specimens. In two small fishes (83 and 108 mm.) the caudal lobes are edged in brown ; in the remainder, the fins are hyaline.

SIZE : 460 mm.

DISTRIBUTION : India, Malay Peninsula, Singapore, Pinang, East Indies, Siam, Formosa, China (Fowler, 1941).

TYPE MATERIAL : Bertin (1940) listed for this species only the holotype and paratypes of *Alausa argyrochloris* Valenciennes (discussed above). Dr. Blanc informs me that there are in fact two (dry) Valenciennes specimens in the Paris Museum (460 mm. *ex* Pondicherry, coll. Leschenault, No. 3939 ; and 440 mm. *ex* Bombay, coll. Roux, No. 3940), and has kindly examined them for me. Head lengths (24·3 and 25·0 per cent. of standard length respectively) confirm that the specimens are *H. toli* and not *H. ilisha*. Unfortunately, the caudals are both damaged (21·6 and 25·0 per cent. of S.L.) and the scale counts (39 and 39) are likely to be a little low. Since the locality and collector of the first fish (No. 3939) are those first mentioned by Valenciennes, this specimen is here designated lectotype.

Study Material.

*2 fishes, 83–108 mm., (Waterhouse collection—no locality) (1858.8.15.68–9).
1 fish, 121 mm., HOLOTYPE of *Alausa argyrochloris* (M.N.H.N.Paris No. 2738).
1 fish, 312 mm., HOLOTYPE of *Alausa ctenolepis* Bleeker, no locality (1867.11.28.23).
†1 fish, 216 mm., Pondicherry, coll. Bélanger (M.N.H.M.Paris No. 3687).
2 fishes, 122–124 mm., Orissa (1889.2.1.1984–5).
2 fishes, 276–396 mm., Bombay (1889.2.1.2018–19).
2 fishes, 110–163 mm., Bombay (1889.2.1.2020–21).

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*Günther's *Clupea chapra* (Catalogue, p. 447).

†1 fish, 314 mm., Bombay, coll. Dussumier (M.N.H.N.Paris No. 3684).
(Dry specimens)
? 1 skin, 225 mm., Ikan Truboh (Cantor collection) (1860.3.19.438).

Gudusia Fowler

Gudusia Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 207 (type, *Clupanodon chapra* Hamilton-Buchanan).

Indo-Pacific alosinid fishes with very small scales, 80–100 in lateral series, 27–35 in transverse series. Scales adherent. Sub-operculum subrectangular or crescentic, its junction with the operculum, if produced, cutting the dorsal outline near or in front of the dorsal origin (Figure 5B).

Branchiostegal rays 6. Gillrakers numerous, 200 or more on lower part of first arch. Dorsal rays 14–16, pelvic 8, anal 20–24. Ventral scutes, 18–20 pre-pelvic and 8–10 post-pelvic.

Two species recognised here, from the rivers of India and Burma.

1 Depth less than 40 per cent. of S.L.; head more than 28 per cent.; anal iii 19–22 ***G. chapra***

2 Depth more than 40 per cent. of S.L.; head less than 28 per cent.; anal iii 22–26 ***G. variegata***

Gudusia chapra (Ham. Buch.)

Clupanodon chapra Hamilton-Buchanan, 1822, *Fishes of the Ganges* : 248, 383, (type locality, Upper Ganges).
Alosa chapra : Gray, 1832–34, *Illustr. Indian Zool. Hardwicke*, **2** : pl. 92, fig. 2.
Alausa chapra : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 440.
Clupea chapra : Day, 1869, *Proc. zool. Soc. London* : 385 ; *Idem*, 1878, *Fishes of India*, pt. 4 : 639, pl. 161, fig. 1 ; *Idem*, 1889, *Fauna British India, Fishes*, **1**: 375.
Gudusia chapra : Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 207 ; Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 307 ; Fowler, 1938, *List. Fish. Malaya* : 26 ; *Idem*, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 634.
Gadusia chapra : Chaturvedi, 1959, *Indo-Pac. Fish. Counc. Occ. Paper* 60/2 : 2 (misspelling).
Clupea indica Gray, 1832–34, *Illustr. Indian Zool. Hardwicke*, **2** : pl. 19, figs. 1–2x ; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 444 ; Beavan, 1877, *F-water Fish. India* : 118.
?Clupea champil Gray, 1832–34, *Illustr. Indian Zool. Hardwicke*, **2** : pl. 91, figs. 5–6.
?Pellona champil : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 324 (on Gray).
Alausa microlepis Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 439 ; Bleeker, 1853, *Verh. Bat. Gen.*, **25** : 146.
Clupea suhia Chaudhuri, 1912, *Rec. Ind. Mus.*, **7** : 436, pl. 38, fig. 1.

Note on synonymy.

Günther's description of *Clupea chapra* seems to refer to a species of *Hilsa* (scales 42, 13 post-pelvic scutes, anal 19) ; the two specimens listed by Günther are *H. toli*.

Alausa champil Cantor is based on two (dry) specimens which are in fact *Kowala thoracata* Valenciennes. *Clupea champil* Gray is based on a drawing which Cantor (1850) believed to be an " indifferent copy " of one in Hamilton-Buchanan's duplicate (and unpublished) series, labelled by Buchanan " *Clupea champil* B." The drawing can only doubtfully be identified with *Gudusia chapra*.

Some Indian workers have referred to *Gadusia*, but this is incorrect.

†Valenciennes' *Alausa palasah* (1847, p. 433).

DESCRIPTION. Based on 10 fishes, 92–140 mm. standard length from Allahabad (Ganges) and Gowhatty (see list of Study Material).

In percentages of standard length : body depth 32·5–40·0 (see also Figure 13), head length 28·2–30·2 ; snout length 5·0–6·3, eye diameter 7·3–8·5, maxilla length 10·4–12·6 ; operculum, height 13·2–13·6, breadth 6·8–7·3 ; pectoral length 20·2–21·2, pelvic length 11·3–11·7, caudal length 30·0–30·3 ; pre-dorsal distance 48·6–52·5, pre-pelvic distance 49·0–51·7. In relation to standard length, eye diameter and maxilla length show negative allometry.

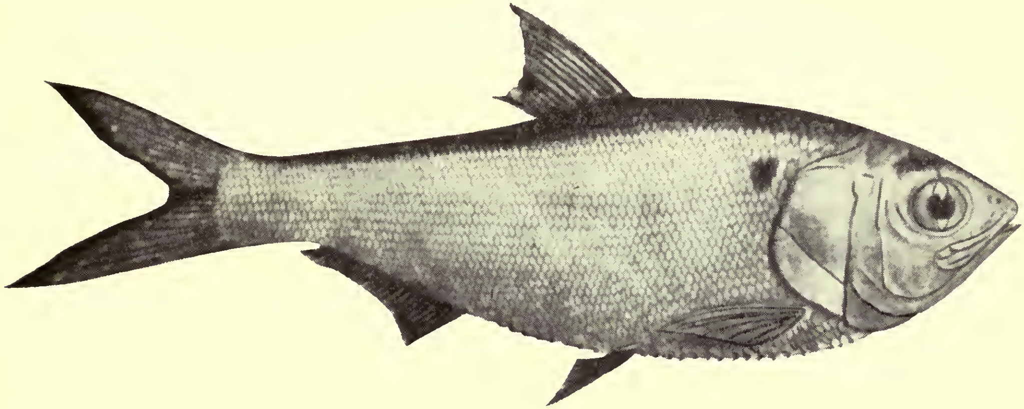

FIG. 11. *Gudusia chapra* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth greater than head length. Snout less than eye diameter ; pre-orbital length (including eye) just less than post-orbital length. Lower jaw included when mouth shut ; maxilla length four-fifths of pre-orbital length, extending to below eye centre or posterior rim of pupil ; exposed portion without longitudinal ridges or striae ; two supra-maxillae. Pseudobranch attenuated, with groove below, as in *Hilsa ilisha* (Figure 6A). Dorsal without low scaly sheath ; dorsal origin more or less equidistant between snout tip and base of caudal ; pelvic origin below unbranched dorsal rays or just in front, a little nearer to snout tip than to caudal base. Pectorals almost reaching pelvic base ; axillary scale present, one-third to one-quarter length of fin. Pelvic fins half length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, about one-third length of fin. Anal fin without scaly sheath ; anal origin equidistant between pelvic base and caudal base ; anal base slightly shorter than in *G. variegata*, about three-quarters to four-fifths pectoral length and usually shorter than the distance snout tip to posterior margin of pre-operculum. Caudal fin just less than head length, lower lobe longer than upper.

No teeth. Cutaneous canals of head branching over sub-orbitals, pre-operculum, operculum and onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil.

Dorsal surface of head covered by skin, but fronto-parietal striae exposed (Figure 1C). Cleithral lobe not prominent, scarcely breaking cleithral outline. Gill filaments of outer hemibranch of first arch half to three-quarters length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, not curled outwards, about as long as corresponding gill filaments in adults. Bones of opercular series as in Figure 5B, the upper (exposed) margin of the suboperculum rising at a steep angle (to cut dorsal profile before dorsal origin if projected).

Dorsal iv 11–13 (first unbranched ray minute), pelvic i 7, anal (ii) iii 19–22, branchiostegal rays 6. Pre-pelvic scutes 17–19, post-pelvic 10 (11), total 27–29. Scales in lateral series 75–100, 27–34 in transverse series (Regan) ; exposed edge of scale smooth ; minute scales covering caudal except along posterior border. Gillrakers fine and numerous, 200 or more on lower part of first arch (Regan).

The pharyngeal pockets of *G. chapra* have been described by Kapoor (1954, 1957), the morphology of the swim-bladder by Srivastava (1956), and the structure of the alimentary tract by Srivastava (1957).

COLOUR : In alcohol, back brown, flanks silvery or golden, a series of faint black spots along upper flank ; caudal edge black.

SIZE : 140 mm. (up to 8 inches—Day, 1889).

DISTRIBUTION : " Freshwaters of rivers and tanks in Sind and throughout India as far south as the Kistna river ; absent from the Malabar coast and Madras " (Day, 1889).

Study Material.

1 fish, 85 mm., Cachar (Assam) (1867.2.14.36).
1 fish, 122 mm., Gowhatty (1889.2.1.1952).
1 fish, 102 mm., Lahore (1889.2.1.1953).
1 fish, 76 mm., Goalpara (1889.2.1.1954).
2 fishes, 69–76 mm., Brahmaputra (1889.2.1.55–56).
5 fishes, 37–105 mm., Orissa (1889.2.1.57–61).
17 fishes, 46–140 mm., Allahabad, Ganges (1934.10.17.1–10) (7 unregistered).
2 fishes, 41–49 mm., Assam (1963.8.23.1–2).
2 fishes, 99–111 mm., India (1963.8.23.3–4).
(Dry specimens)
1 fish, 148 mm., Ganges (1848.2.1.67).
1 fish, 151 mm., no locality, India House collection (1860.3.19.676).

Gudusia variegata (Day)

Clupea variegata Day, 1869, *Proc. zool. Soc. London* : 623 (type locality, Irrawaddy river, Burma) ; *Idem*, 1878, *Fishes of India*, pt. 4 : 639, pl. 161, fig. 4 ; *Idem*, 1889, *Fauna Brit. India, Fishes*, **1** : 375 ; Vinciguerra, 1890, *Ann. Mus. Civ. Stor. nat. Genova*, (ser. 2) **9** : 350 ; Lloyd, 1907, *Rec. Ind. Mus.*, **1** : 221 ; Jenkins, 1910, *Rec. Ind. Mus.*, **5** : 138.

Gudusia variegata : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 308 ; Myers, 1924, *Amer. Mus. Nov.*, No. 150 : 1 ; Prashad & Mukerji, 1929, *Rec. Ind. Mus.*, **31** (3) : 209 ; Fowler. 1941, *Bull. U.S. nat. Mus.*, No. 100 : 635.

DESCRIPTION. Based on a single fish, 155 mm. standard length from Bassein (Burma).

In percentages of standard length : body depth 41·6, head length 27·7 ; snout length 5·9, eye diameter 6·4, maxilla length 11·5 ; operculum, height 13·3, breadth 6·9 ; pectoral length 18·2, pelvic length 11·3, caudal length 30·1 ; pre-dorsal distance 49·5, pre-pelvic distance 52·2.

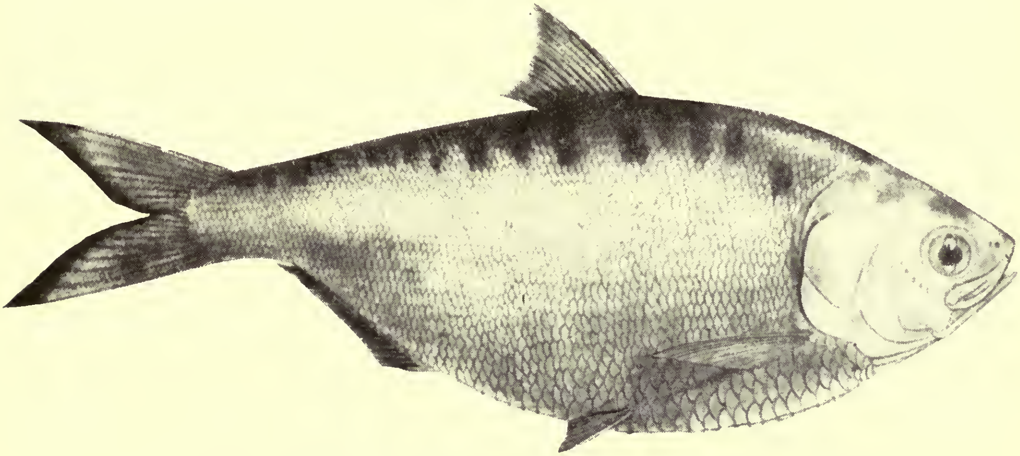

FIG. 12. *Gudusia variegata* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth one and a half times head length. Snout less than eye diameter ; pre-orbital length (including eye) three-quarters of post-orbital length. Lower jaw included when mouth shut ; maxilla length almost equal to pre-orbital length, extending just beyond eye centre ; exposed portion without longitudinal ridges or striae. Pseudobranch attenuated, with groove below as in *Hilsa ilisha* (Figure 6A). Dorsal with very small scaly sheath ; dorsal origin about equidistant between snout tip and base of caudal ; pelvic origin below unbranched dorsal rays, a little nearer to snout tip than to base of caudal. Pectorals not reaching pelvic base ; axillary scale present, about half length of fin. Pelvic fins a little over half length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, almost half length of fin. Anal fin with very low scaly sheath ; anal origin equidistant between pelvic base and caudal base ; anal base exceeds pectoral length and exceeds distance snout tip to posterior border of pre-operculum. Caudal fin a little greater than head length, lower lobe longer than upper.

Teeth absent, except minute teeth on tongue. Cutaneous sensory canals of head branching over suborbitals, pre-operculum, operculum and onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil.

Dorsal surface of head covered by skin, but fronto-parietal striae exposed (see Figure 1C). Cleithral lobe not prominent, scarcely breaking cleithral outline. Gill filaments of outer hemibranch of first arch half to three-quarters length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, not curled outwards, about as long as corresponding gill filaments. Bones of opercular series as in Figure 5B, the upper (exposed) margin of the sub-operculum rising at a steep angle (to cut dorsal profile before dorsal origin if projected) ; sub-operculum almost crescentic.

Dorsal iv 12 (first unbranched ray minute), pelvic i 7, anal iii 22, branchiostegal rays 6. Pre-pelvic scutes 19, post-pelvic 11, total 30. Scales in lateral series 90, 32 in transverse series (Regan) ; exposed part of scale with a single prominent vertical striation ; edge of scale pectinated ; minute scales covering caudal except along posterior border.

Colour : In alcohol, brown on back, flanks golden, a series of brown spots along upper flank, some expanded vertically, those behind dorsal extending right across back ; dark spot at base of posterior dorsal rays ; caudal tips colourless (" tipped with black "—Day 1869).

Size : 155 mm. (7 inches, Day 1869).

Distribution : Rivers of Burma.

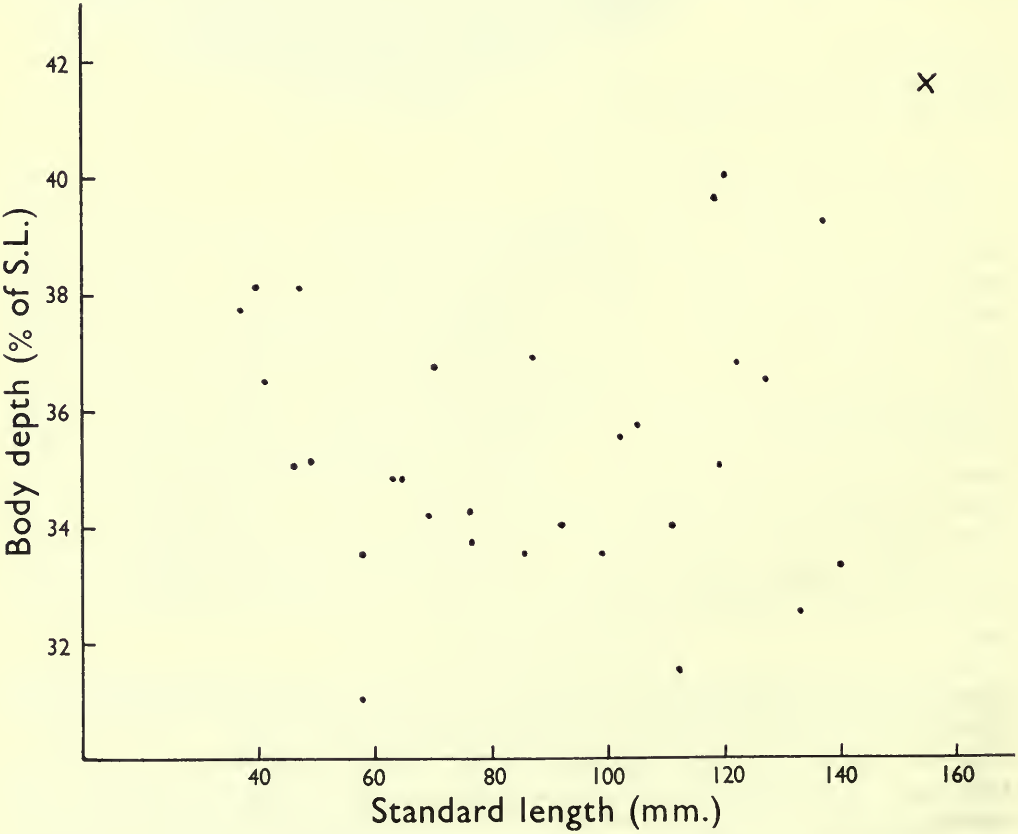

Fig. 13. Body depth as a percentage of standard length, plotted against standard length for species of *Gudusia*.
× *G. variegata* ● *G. chapra*

Relationship to G. chapra.

The differences separating this species from *G. chapra* are small, and it is possible that, when more specimens are available, *G. variegata* will be regarded merely as an eastern form or subspecies of *G. chapra*. The difference in body depth may perhaps be due to allometric growth, since the specimen of *G. variegata* is the largest examined. In Figure 13 body depth as a percentage of standard length is plotted against standard length for 30 specimens of *G. chapra* and 1 of *G. variegata*. The points are rather scattered, but the graph suggests that the body is relatively deeper in fishes below 50 mm. and also in those above 120 mm.

Other differences between *G. variegata* and *G. chapra* are the smooth-edged scales in the latter and perhaps colouration.

THE WEST AFRICAN GENUS *ETHMALOSA*

As noted earlier, the West African genus *Ethmalosa* resembles the Indo-Pacific Alosinae (*Hilsa* and *Gudusia*), and differs from the Atlantic, Mediterranean and New World Alosinae, in two characters, Regan's gillraker character and pelvic fin ray count (8 ; *cf* 7 or 9). However, the weight attached to these two characters as indicators of probable phyletic relationships must first be viewed in the light of possible zoogeographical relationships.

In general, the clupeoid fauna of West Africa is poor in both species and genera when compared with that of either the New World or the Indo-Pacific. Thus, there are no West African gizzard shads (Dorosomatinae), or round herrings (Dussumieriidae), and only a single engraulid genus, the widespread *Engraulis*, with a single species close to the North Atlantic *E. encrasicolus* (Whitehead 1964b). In the subfamily Clupeinae, records of *Sardina pilchardus* have probably been based on one or two stray fishes from the North Atlantic. *Sardinella*, however, with two species, *S. aurita* Valenciennes and *S. maderensis* (Lowe), is principally an Indo-Pacific genus. *S. maderensis* (for which *S. eba* [Valenciennes], *S. granigera* Valenciennes and *S. cameronensis* Regan are probably synonyms) occurs only off the West African coast and in the Mediterranean, but *S. aurita* is found along the Atlantic coast of America, in the Mediterranean, and also in the Western Pacific (Japan, Philippines). *S. aurita* is, however, replaced in the Indian Ocean by *S. longiceps* Valenciennes. *Harengula*, a Western Atlantic genus, is not represented in West Africa ; *H. rouxi* Poll is a species of *Sardinella* (Whitehead 1964a). The subfamily Pellonulinae shares no genera with the Indo-Pacific.

Finally, in the subfamily Pristigasterinae, the genus *Ilisha* is shared both with the Indo-Pacific and with the Western Atlantic. But Tucker (1954) believed the West African species, *I. africana* (Bloch), to be more closely allied to the species and genera of the Atlantic coast of South America than to any Indo-Pacific form. He felt that there might one day be a case for recognising the distinctness of the West African *I. africana* from the Indo-Pacific forms by the creation of a new subgenus.

Thus, only two West African clupeid genera are shared with the Indo-Pacific. But they are also the only two Western Atlantic clupeid genera which are found in West Africa ; and at species level both show closer links with the Western Atlantic than with the Indian Ocean. On zoogeographic grounds, therefore, *Ethmalosa* would be expected to show less affinity with the Indo-Pacific than with the New World genera.

Against this argument, there is further morphological evidence linking *Ethmalosa* with the Indo-Pacific Alosinae. The fronto-parietal striation pattern is identical to that found in *Hilsa kelee* (but it also resembles that in *Brevoortia*). Perhaps more significant, the rather characteristic gillrakers on the upper parts of all arches and the lower parts of the third and fourth arches in *Ethmalosa* may well represent merely an extreme form of the curled gillrakers found in *Hilsa kelee*. The pseudobranch in *Ethmalosa* also resembles that of *H. kelee*. On the other hand, the maxilla in *Ethmalosa* is smooth (but ridged in *Brevoortia*) and the cleithral lobe is little developed (as in *Brevoortia, Alosa*).

On present evidence therefore, the question must remain open. *Ethmalosa* may have been derived from the Western Atlantic, or from the Indian Ocean, or it might represent an independent relict of a once widespread alosinid fauna. Until this problem can be solved, a tribal division in the Alosinae would be unrealistic.

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A CRITICAL REVIEW OF THE MARINE NEMATODE GENUS *EUCHROMADORA* DE MAN, 1886

By JOHN W. COLES

SYNOPSIS

Seven species of *Euchromadora*, two of which are new, are described : *E. vulgaris* (Bastian, 1865) [type species] ; *E. adriatica* (v.Daday, 1901) ; *E. gaulica* Inglis, 1962 ; *E. loricata* (Steiner, 1916) ; *E. scampae* sp. nov. ; *E. shirleyae* sp. nov. and *E. striata* (Eberth, 1863). On the basis of their study a general account of the morphology of the genus is given and the genus diagnosed. *Euchromadora* is characterized chiefly by (1) the complicated structure of the cuticle, with transverse rows of large oval to hexagonal markings at the anterior end of the body which become elongate posteriorly ; and (2) the shape of the male genital apparatus, which supplies the most important characters in the delimitation of species. The remaining nominal species are reviewed and only eight are considered valid : *E. amokurae* (Ditlevsen, 1921) ; *E. archaica* Steiner and Hoeppli, 1926 ; *E. chitwoodi* nom. nov. [=E. *striata of* Chitwood, 1951] ; *E. inflatispiculum* Schuurmans Stekhoven, 1943 ; *E. mediterranea* Allgén, 1942 ; *E. parafricana* Gerlach, 1958 ; *E. permutabilis* Wieser, 1954 ; *E. tokiokai* Wieser, 1955. *E. tridentata* of Wieser, 1951 [nec Allgén, 1929] is considered a synonym of *E. gaulica* and *E. tyrrhenica* Brunetti, 1952 a synonym of *E. adriatica*. All nomenclatorial changes are listed on page 191.

INTRODUCTION

THE genus *Euchromadora*, which was erected by de Man in 1886 for *Chromadora vulgaris* Bastian, 1865, contains some of the largest members of the family Chromadoridae. Species are commonly found among the finer marine algae which constitute a major part of their food. De Man's diagnosis of the genus is based on his (1886) description of *E. vulgaris*, which is very detailed with magnificent figures, in marked contrast to the inadequacy of nearly all the descriptions published since then. In this diagnosis he stresses : (1) the very complex cuticle, (2) the form of the head with a movable dorsal tooth, (3) the gradual posterior swelling of the oesophagus which does not form a definite bulb, (4) the absence of pre-cloacal supplements in the male and (5) the unequal and dissimilar spicules, a character he particularly stresses. Some species now referred to *Euchromadora* were originally placed in the genus *Spilophora* Bastian, 1865 including *S. loricata* Steiner, 1916. However, soon after describing this species Steiner (1918), from a study of six species from the west coast of Africa, modifies the diagnosis of *Euchromadora*. He considers the genus should not be restricted by (3) and (5) above, i.e. the form of the oesophagus and the inequality of the spicules, because *Spilophora loricata*, although having a pronounced posterior oesophageal bulb and equal spicules, is in all other respects a typical *Euchromadora*. He therefore expands the concept of *Euchromadora* to include this species. Filipjev in the same year (1918) independently reaches the same conclusion after studying specimens of *Odontobius striatus* Eberth, 1863, and refers this species to *Euchromadora*. More recently Wieser (1954) reviews the genus (with a key) in a successful attempt to bring some order to it.

I have studied specimens of seven species of *Euchromadora* from the coasts of the British Isles (all among algae) ; Spitzbergen ; Banyuls-sur-Mer, France and from off the coast of South Africa, thus : *E. vulgaris* (Bastian, 1865) ; *E. adriatica* (v. Daday, 1901) ; *E. gaulica* Inglis, 1962 ; *E. loricata* (Steiner, 1916) ; *E. scampae* sp. nov. ; *E. shirleyae* sp. nov. and *E. striata* (Eberth, 1863). These species are described below in detail and on the basis of the data so obtained the remaining species of the genus are reviewed.

MORPHOLOGY

General Form and Cuticle.

The general shape of the body which is illustrated in Text-fig. 22 (*E. gaulica*) appears to be a reflection of the structure of the cuticle as is suggested by Steiner and Hoeppli (1926). Superficially the dark amber cuticle appears to be marked by coarse transverse striations (in *E. vulgaris* such striations are about 3µ apart at the anterior end near the head, 4µ at the posterior end of the oesophagus, 5µ on the mid-body region and 4µ apart at the anal region). At the head end a few uneven rows of small circular punctations occur in the cuticle before the striations become apparent anteriorly. There is, however, some variation according to the degree of contraction or expansion of the head. Associated with the striations, posterior to the circular punctations, are the oval to hexagonal markings so very characteristic of the genus. Inglis (1964a), who has made a most detailed study of the cuticle of this genus, shows that the cuticle is composed of an external and an internal series of transverse rings which are joined together by a series of rods. The external rings are slightly anterior to the internal rings and are wedge-shaped in section. The thin edge of the wedge projects over the stoutly rounded posterior edge of the immediately preceding ring, on the anterior part of the body. On the posterior part of the body the conditions are reversed, and in the female this change takes place at the vulva. Projecting from the intermediate connecting rods are anteriorly-directed processes of dense material which, in plan view, are seen as the characteristic hexagonal markings. De Man (1886) figures these markings with lines connecting each row giving the appearance of a basket-work formation which, as Inglis (1964a) points out, is probably an optical illusion. It has already been shown that the various components of the cuticle are at different levels. In their study of *E. archaica* Steiner and Hoeppli (1926) consider that the significance of the hexagonal formations is for stiffening and adding strength to the cuticle, but Inglis refines this argument in terms of the conflicting demands of tangential stress and longitudinal flexibility.

Farther posteriorly, about the posterior end of the oesophagus, the hexagonal markings become increasingly elongate. On the lateral surfaces this condition exists along the length of the body, while on the dorsal and ventral surfaces the markings become restricted to certain regions of the body. In most species, on the dorsal and ventral surfaces, commencing at the anterior region where the oesophagus narrows a little, two zones occur without hexagonal markings, and these widen very gradually till near the posterior end of the oesophagus (see Text-fig. 1). The markings between these two regions (i.e. on the mid-dorsal and mid-ventral surfaces) then become narrower and disappear over a tapering zone. This middle part is then devoid of markings until just beyond the cloaca or anus, when they reappear over a similar tapering zone to surround the body again in the tail region. However, in one species (*E. shirleyae*), the markings between the two clear zones, on the dorsal and ventral surfaces, continue throughout the length of the worm (see Text-fig. 8). In larval specimens no such differentiation occurs and the punctation markings are small and oval, lending support to Inglis' argument that the elaborations of the adult cuticle derive from a system of simple punctation rods and canals.

In some species other modifications are seen, deep within the cuticle, on the lateral surfaces. They have been referred to by Steiner (1918) and Micoletzky (1924) as ' articulation structures ' and by Inglis (1962) as ' lateral plates '. They are seen in some specimens much more clearly than in others, and depending on the condition of the specimen and the observer, can be interpreted differently. Micoletzky (1924) notes that they form a kind of lateral membrane over about 30 per cent. of the diameter of the body and are probably formed with the last moult. These modifications occur on the inner solid transverse rings (? basal layer) which Inglis (1964a) describes. The centre portion of each ' plate ', through which runs a minute pore, curves anteriorly on its anterior edge at the anterior end of the body, while on the posterior part of the body the conditions are reversed (see Text-fig. 6). In the female the change over takes place at the vulva. In some species such ' lateral plates ' have not been seen at all, for example, in *E. archaica* according to Steiner and Hoeppli (1926). Instead these authors figure a series of curved lines on the lateral surfaces and I have noted that it is the same in *E. adriatica*.

Ocelli have been observed at the anterior end in some specimens of *E. vulgaris* and *E. striata*, but it appears that the pigment often dissolves out on preservation so that the ocelli become invisible. Body setae are usually present. In *E. vulgaris* and *E. striata* they occur at the anterior end of the body in four files of twelve to fifteen setae (corresponding approximately to the four cephalic setae) about 30μ apart and extending to the level of the anterior end of the intestine. Posterior to this region in both these species setae occur only sporadically. However in all other species setae occur sporadically over the whole length of the body, including the oesophageal region. It is probable that they are frequently lost during collection, fixation and subsequent processing. There are nearly always two pairs of setae near the tip of the tail. One pair projecting dorsally and the other pair projecting ventrally (Text-fig. 3). The tail in both sexes is usually fairly long, but species differ a little in this respect. The usual three caudal glands are present, posterior to the anal region and a well marked spinneret is present.

Head structures.

The head is very blunt, a character, which in conjunction with the dark cuticle, is useful when sorting specimens under a dissecting microscope. The mouth opening is surrounded by a rather poorly defined cuticular sheath which is supported by the twelve rugae typical of the family. There are two circles of six head papillae, those of the inner circle are very small (not seen in the smaller species but most likely present) and those of the outer circle are prominent and setose. Farther posteriorly are four long cephalic setae dorso- and ventro-lateral in position, which are about 10μ to 15μ long. Laterally, at this same level, are the two crescent-shaped or slit-like amphids. The anterior end of the oesophagus forms a conical ' onchial cavity ' (terminology of Inglis (1964)) at the anterior edge of which is a large dorsal tooth (onchium), together with subventral plates, denticles and other variable cuticular structures. The edges of the ventro-lateral sectors of the oesophagus are thickened at the base of the onchial cavity to form horizontal rod-like cuticular structures. These structures can only be seen with very great difficulty in *en face* view because, as lateral views establish, they lie slightly posterior to the dorsal onchium and the other structures developed on the ventro-lateral walls of the onchial cavity. The dorsal onchium belongs to what Wieser (1954) calls the ' solid type '. The whole of the mouth region (rugae, anterior end of the oesophagus) is flexible to enable the onchia to extrude and this causes the outline of the head to vary in different specimens.

Oesophagus and Intestine.

The oesophagus narrows a little behind the onchial cavity and in some species is provided with a well defined posterior bulb, in some it widens very gradually towards the posterior end, while in one, *E. shirleyae*, it is of almost even width throughout its length. The nerve ring is situated a little in front of half the length of the oesophagus and is not always easily seen. The excretory pore, which in some species is not seen, is situated just a little posterior to the nerve ring. A seta-like appendage about 2μ to 3μ long is situated at the mouth of the excretory pore in *E. vulgaris* and *E. striata* and at about 1·5 times the diameter of the head from the anterior end (ventrally) in *E. gaulica*. Cobb (1914) mentions the occurrence of this appendage in his description of *E. denticulata* and *E. meridiana* and Micoletzky (1924) also found it on his specimens of *E. striata* from Suez. The ventral gland, which usually extends to beyond the anterior end of the intestine, is seen more clearly in some species than in others.

Male.

The shape of the male genital apparatus, which is a characteristic feature of this genus, also supplies the most important characters for the recognition of species. The spicules are paired, usually equal in length and identical in structure (in the type-species, however, they are unequal). The gubernaculum consists of a pair of lateral, massive, cuticular, somewhat hammer-shaped, structures which are usually more prominent than the spicules, and a median dorsal piece which is triangular in outline. The single testis is outstretched and its junction with the vas deferens is not clearly defined. Two median pre-cloacal setae are generally present (in one species they are replaced by papillae (see Text-fig. 8) but pre-cloacal sucker-like supplements typical of most genera of the family do not occur.

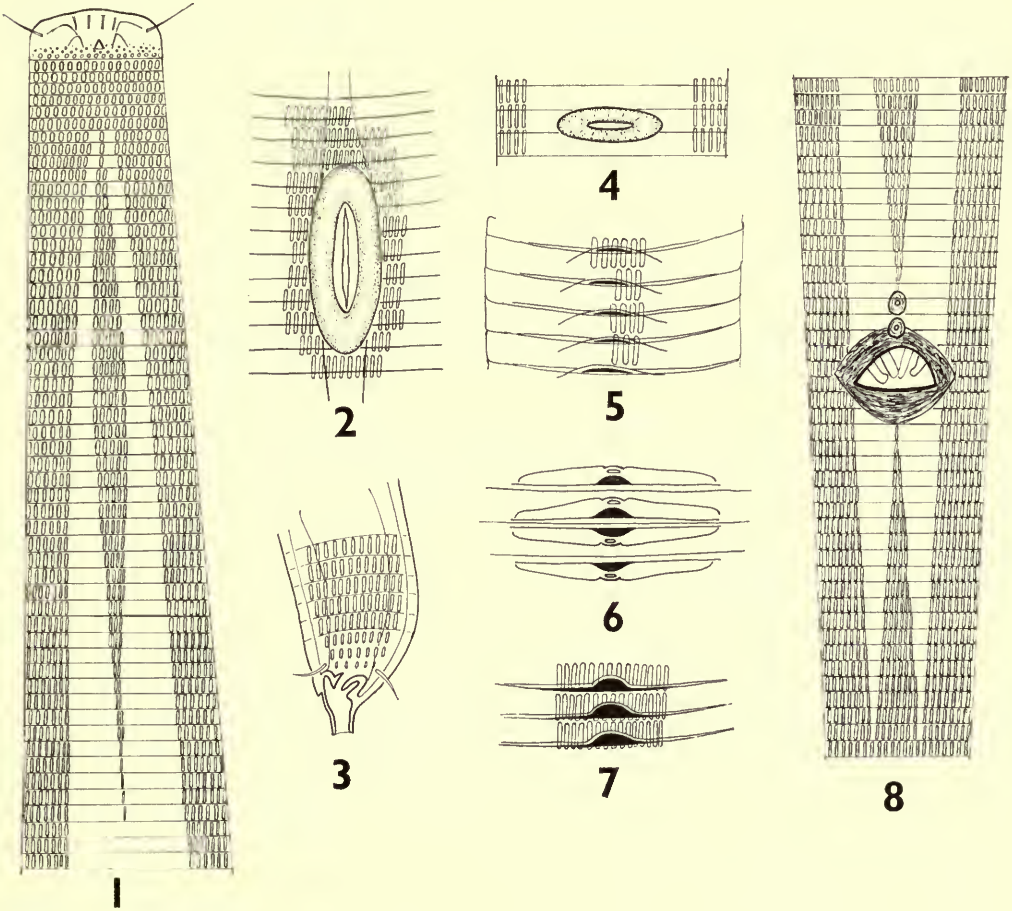


Fig. 1. Diagram of the anterior end of *Euchromadora* spp. to illustrate the arrangement of the cuticular markings on the dorsal and ventral surfaces. Fig. 2. Vulva of *E. shirleyae*. Fig. 3. Posterior extremity of *E. adriatica* (typical of all species studied). Fig. 4. Vulva of *E. vulgaris* (typical of all species studied except *E. shirleyae*). Fig. 5. *E. scampae*. Structures comparable to the ‘ lateral plates ’ just posterior to the oesophagus. Fig. 6. ‘ Lateral plates ’ at approximately the mid-body region of *E. vulgaris*, *E. striata*, *E. gaulica* and *E. loricata*. Fig. 7. *E. vulgaris*. ‘ lateral plates ’, cloacal region. Fig. 8. *E. shirleyae*. Ventral view of the cloacal region to illustrate the arrangement of the cuticular markings and the pre-cloacal papillae. (All Figs. except 2–4 semi-diagrammatic.)

Female.

The female reproductive system is double and the ovaries are opposed and reflexed. Usually about three to six eggs, which measure from about $35\mu \times 32\mu$ to about $90\mu \times 65\mu$, are present in the uteri. Up to nineteen have been seen in one species. The vulva is situated ventrally about the mid-point of the worm and in all the species I have examined, except one, it is a transverse slit relative to the longitudinal axis of the body (Text-fig. 4). In *E. shirleyae* the slit is longitudinal and relatively more prominent (see Text-fig. 2).

DIAGNOSIS OF THE GENUS

Euchromadora appears to be the culmination of an evolutionary trend through *Chromadorita* and *Neochromadora*, in which there is an increasing complexity of the head, spicules and gubernaculum and, particularly, the cuticle. The characteristic morphological features of the genus may be summarised in a diagnosis as follows :

Chromadoridae. Cuticle complicated with transverse rows of large oval to hexagonal markings at the anterior end of the body, which become elongate posteriorly ; onchial cavity with a large solid movable dorsal onchium and various dentate cuticular plates and other cuticular structures ; amphids large crescent-shaped slits.

MALE : Spicules equal or subequal, similar in structure ; gubernaculum present, consisting of prominent paired, somewhat hammer-shaped, lateral pieces and a dorsally situated median plate ; pre-cloacal supplements absent ; testis single and outstretched.

FEMALE : Ovaries paired, opposed, reflexed ; up to nineteen eggs in the uterus, but usually no more than six.

TYPE SPECIES : *Chromadora vulgaris* Bastian, 1865.

CHARACTERS OF IMPORTANCE IN THE DELIMITATION OF SPECIES

Wieser (1954) treats the genus in two groups. In one group the dorsal onchium is large with an enlarged base, and the distal portion is, in most cases, bent and directed anteriorly, and the onchial cavity is heavily sclerotized. In the other group the dorsal onchium is of medium size and not bent, while the onchial cavity is less sclerotized. It is clear that whether the dorsal onchium is pointing anteriorly or not is of no significance because this structure is movable and its position varies from specimen to specimen.

During this study other degrees of cuticularization of the onchial cavity have become apparent which suggest there is a series of forms of increasing complexity. Thus *E. scampae* is the simplest form studied and compares with Wieser's group ' B ' (Text-figs. 16–18), *E. shirleyae* is of intermediate complexity (Text-figs. 19–21), *E. loricata* and *E. adriatica* much more complicated and *E. vulgaris* and *E. striata* (Text-figs. 9–12) the most complicated forms of all. *E. gaulica* is almost as complicated as *E. vulgaris* and *E. striata* but is a smaller species. On the walls of the onchial cavity of these latter species are cuticular plates and rows of small denticles ; situated subventrally are two enlarged double-pointed cuticular plates anterior to the horizontal rod-like structures described on page 162. It would appear that what have frequently been referred to as subventral teeth are in fact these rod-like structures. The enlarged plates are usually more difficult to see in lateral view than in *en face* preparations.

The punctation markings of the cuticle show slight variation in shape at the anterior end of the body ; in some species they are more markedly hexagonal, or even rectangular, than in others. This depends to a certain extent on the focusing as the shape varies a little at different levels, so that this character is of little value in delimiting species. Only one species, *E. shirleyae*, is markedly different from the others in lacking clear zones on the mid-dorsal and mid-ventral surfaces (see page 184).

The most valuable characters for the separation of species are the shape and relative lengths of the spicules, the shape of the gubernaculum, particularly the distal end, and the lengths of the lateral pieces of the gubernaculum relative to the length of the spicules. When only females are available exact determination is, in general, not possible.

Euchromadora vulgaris (Bastian, 1865) de Man, 1886
(Text-figs. 9–12, 24–25)

Chromadora vulgaris Bastian, 1865. *Trans. Linn. Soc. Lond.* **25**, 167–168, pl. 13, figs. 233–235.
Euchromadora vulgaris, de Man, 1886. *Anatomische Untersuchungen über freilebende Nordsee-Nematoden.* Leipzig, 69–75, pls. 12–13.

TYPE LOCALITY : Falmouth, Cornwall, England.

MATERIAL STUDIED : Numerous specimens (12♂♂ 12♀♀, 4 larvae selected at random and measured) from : green or blue-green filamentous algal growth on the sea water circulation benches, Laboratory of the M.B.A., Plymouth, August, 1955 (B.M. (N.H.) Reg. Nos. 1955.11.1. 326–337) ; among *Cladophora rupestris* growing in a rock-pool fairly high on the shore, Wembury Bay, S. Devon, June, 1956 (Reg, Nos. 1963. 525–539) ; among algae, approx. M.L.W.N., Hannafore, Looe, Cornwall. June, 1956 (Reg. Nos. 1963. 540–554) ; among algae incl. *Corallina* sp., rockpool, Black Rock, Brighton, Sussex, August, 1960 (Reg. Nos. 1963. 555–561) ; among filamentous blue-green algae (incl. *Anabaena* ? *torulosa* and *Oscillatoria* sp.) in a rock pool high on the shore, Poyllbrein, south coast, Isle of Man, August, 1961 (Reg. Nos. 1963. 562–566) ; among *Enteromorpha* sp., Falmouth, Cornwall, August, 1960 (Reg. Nos. 1963. 567–570).

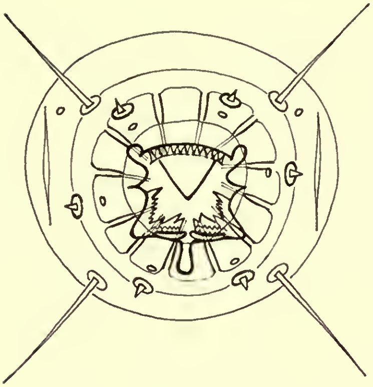
				Body ratios	
	Body length (mm.)	*a*	*b*	*c*	$\frac{\text{length gubernaculum}}{\text{length spicules}} \times 100$
Males	1·85	30·8	5·1	9·7	61·5
	1·85	23·1	5·7	9·7	63·5
	1·85	23·1	5·7	9·7	66·7
	1·90	27·1	5·8	9·0	57·3
	1·92	27·4	5·4	9·8	61·7
	1·94	26·9	5·5	8·8	57·1
	2·10	23·3	6·1	10·5	62·8
	2·15	25·2	5·9	9·7	54·7
	2·17	21·7	6·4	9·0	60·9
	2·23	24·8	6·5	11·7	58·2
	2·27	28·3	5·9	11·3	61·4
	2·35	26·7	6·5	10·7	57·3

					V
Females	1·84	23·0	5·4	9·2	50·0
	1·97	21·9	5·8	8·6	47·7
	2·00	20·0	6·0	8·7	47·5
	2·15	20·5	5·6	8·7	49·3
	2·16	30·0	5·4	9·4	50·9
	2·20	18·3	5·8	8·9	48·2
	2·25	17·3	5·6	9·0	48·0
	2·37	21·2	5·4	8·6	50·2
	2·37	21·5	5·9	8·7	49·3
	2·50	20·8	6·6	9·4	48·0
	2·53	21·1	7·0	9·7	47·4
	2·55	23·2	6·4	9·5	50·9
Larvae	1·00	22·2	4·0	7·1	54·0
	1·02	22·6	4·2	7·3	—
	1·02	22·6	4·1	7·7	—
	1·37	22·4	5·1	9·1	—

Measurements (in mm. in order of body lengths). Males. Body breadth: 0·060 ; 0·080 ; 0·080 ; 0·070 ; 0·070 ; 0·072 ; 0·090 ; 0·085 ; 0·100 ; 0·090 ; 0·080 ; 0·088. Head diameter : 0·032 ; 0·034 ; 0·034 ; 0·033 ; 0·034 ; 0·033 ; 0·040 ; 0·035 ; 0·034 ; 0·035 ; 0·034 ; 0·032. Length of oesophagus : 0·36 ; 0·32 ; 0·32 ; 0·36 ; 0·35 ; 0·35 ; 0·34 ; 0·36 ; 0·34 ; 0·34 ; 0·38 ; 0·36. Length of tail : 0·19 ; 0·19 ; 0·19 ; 0·21 ; 0·19 ; 0·22 ; 0·20 ; 0·22 ; 0·24 ; 0·19 ; 0·20 ; 0·22. Cloacal diameter : 0·050 ; 0·055 ; 0·056 ; — ; 0·055 ; 0·055 ; 0·070 ; 0·060 ; 0·065 ; 0·067 ; 0·057 ; 0·055. Length of spicules : 0·065 ; 0·063 ; 0·063 ; 0·075 ; 0·060 ; 0·070 ; 0·070 ; 0·075 ; 0·069 ; 0·067 ; 0·070 ; 0·075. Length of gubernaculum (lateral pieces) : 0·040 ; 0·040 ; 0·042 ; 0·043 ; 0·037 ; 0·040 ; 0·044 ; 0·041 ; 0·042 ; 0·039 ; 0·043 ; 0·043. Distance of nerve ring from anterior end : — ; 0·152 ; 0·149 ; — ; 0·150 ; — ; — ; 0·152 ; — ; 0·130 ; 0·160 ; 0·143. Distance of excretory pore from anterior end : 0·155 ; — ; 0·180 ; — ; 0·165 ; — ; — ; 0·163 ; — ; 0·159 ; 0·180 ; 0·175.

Females. Body breadth : 0·080 ; 0·090 ; 0·100 ; 0·105 ; 0·072 ; 0·120 ; 0·130 ; 0·112 ; 0·110 ; 0·120 ; 0·120 ; 0·110. Head diameter : 0·034 ; 0·033 ; 0·035 ; 0·033 ; 0·036 ; 0·038 ; 0·040 ; 0·038 ; 0·037 ; 0·045 ; 0·036 ; 0·038. Length of oesophagus : 0·34 ; 0·34 ; 0·33 ; 0·38 ; 0·40 ; 0·38 ; 0·40 ; 0·44 ; 0·40 ; 0·38 ; 0·36 ; 0·40. Length of tail : 0·20 ; 0·23 ; 0·23 ; 0·25 ; 0·23 ; 0·24 ; 0·25 ; 0·27 ; 0·27 ; 0·26 ; 0·26 ; 0·27. Anal diameter : — ; 0·041 ; 0·040 ; 0·044 ; 0·050 ; 0·050 ; 0·058 ; 0·055 ; 0·060 ; — ; 0·050 ; 0·050. Distance of vulva from anterior end : 0·92 ; 0·94 ; 0·95 ; 1·06 ; 1·10 ; 1·06 ; 1·08 ; 1·19 ; 1·17 ; 1·20 ; 1·20 ; 1·30 . Distance of nerve ring from anterior end : 0·150 ; — ; — ; 0·160 ; 0·163 ; — ; 0·161 ; — ; — ; — ; 0·140 ; —. Distance of excretory pore from anterior end : 0·165 ; — ; 0·125 ; 0·180 ; — ; — ; 0·182 ; — ; 0·180 ; — ; 0·170 ; —.

Larvae. Body breadth : 0·045 ; 0·045 ; 0·045 ; 0·061. Head diameter : 0·030 ; 0·031 ; 0·032 ; 0·032. Length of oesophagus : 0·25 ; 0·24 ; 0·25 ; 0·27. Length of tail : 0·13 ; 0·14 ; 0·13 ; 0·15.



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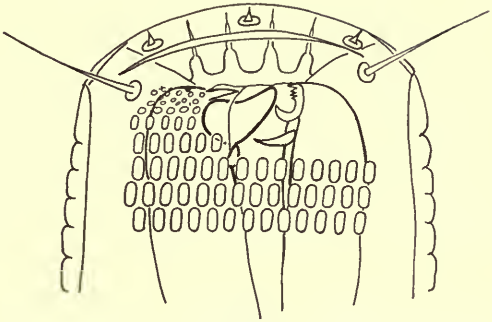

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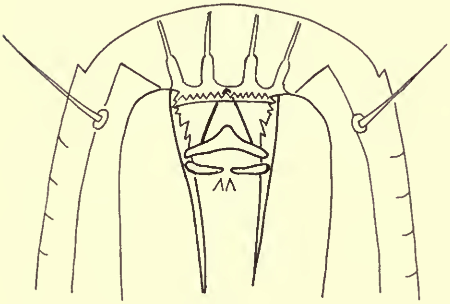

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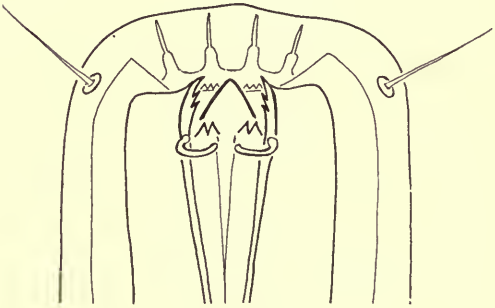

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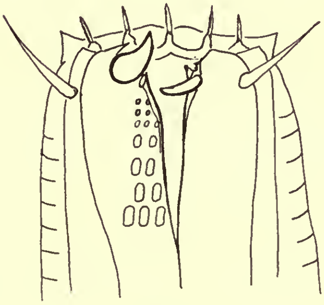

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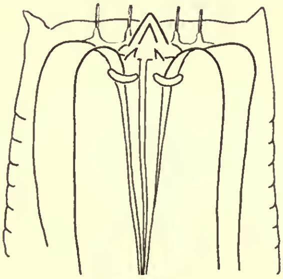

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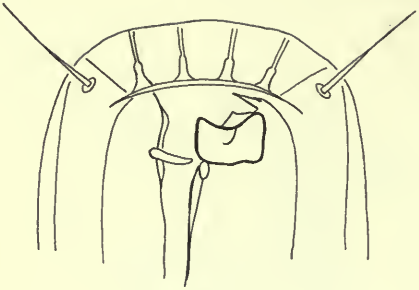
FIGS. 9–12. *E. vulgaris.* Fig. 9 *En face* view of head. Fig. 10. Lateral view of head. Fig. 11. Dorsal view of head. Fig. 12. Ventral view of head. FIGS. 13–14. *E. gaulica.* Fig. 13. Lateral view of head. Fig. 14. Ventral view of head. (All to same scale.)



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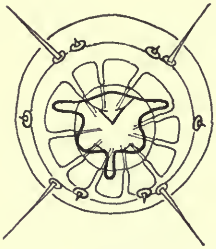

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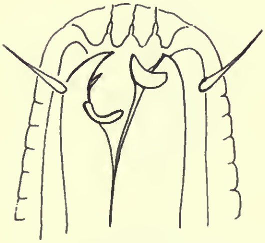

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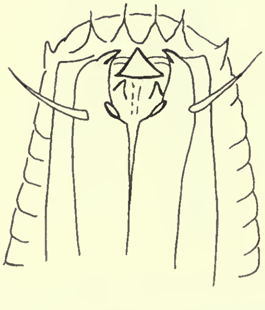

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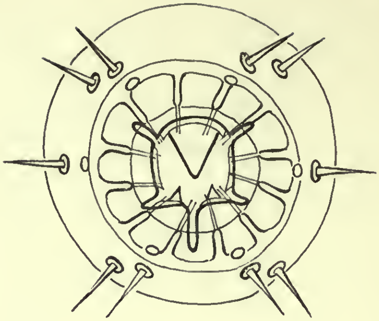

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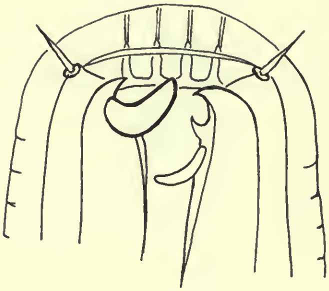

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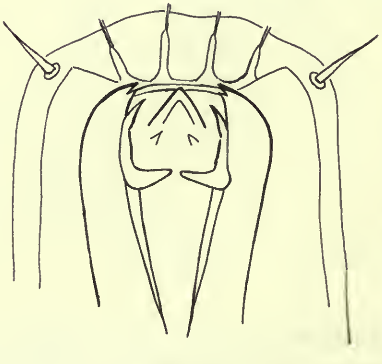

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GEOGRAPHICAL DISTRIBUTION. NORWAY : Vega, Gasnes, Ingoy and Stappen etc. (Allgén, 1940, 1943, 1946, 1951a) ; SWEDEN : West coast, vicinity of the Zoological Station, Kristineberg (Allgén, 1929, 1929b, 1951, 1953). DENMARK : Limfjord and Kattegat (Ditlevsen, 1919) ; HOLLAND : Walcheren (de Man, 1886), coast of Zeeland (de Man, 1907, 1907a ; oyster-beds, Yerseke (Schuurmans Stekhoven, 1942) GERMANY : Insel Amrum, Schleswig-Holstein etc. (Gerlach, 1953, 1954). FRANCE : Coast of Britanny (Ditlevsen, 1923). BRITISH ISLES : Falmouth (Bastian, 1865) ; Plymouth (Wieser, 1951, 1952) ; Whitstable (Maghraby and Perkins, 1956) ; Coast of southern England and Isle of Man (present author, see above) ; West coast of Ireland—Blacksod Bay, Clew Bay—shores of Clare I. and Annagh I. (Southern, 1914).

DISTINCTIVE CHARACTERS. Cuticle : ' Lateral plates ' present. Cephalic setae : 12μ. Head and oesophagus : The onchial cavity is complicated, with cuticular plates and rows of denticles on the inside walls. Two enlarged double-pointed cuticular plates are situated subventrally, opposite the dorsal onchium (as described on page 164) (Text-figs. 9–12). The oesophagus widens gradually towards the posterior end, without forming a distinct bulb. The ventral gland is indistinct, extending to the posterior end of the oesophagus or to the anterior end of the intestine. A seta-like appendage is situated at the mouth of the excretory pore.

MALE : The spicules, which carry fine alae, are unequal in length but similar in shape. The smaller left spicule is about 85 per cent. of the length of the longer, i.e. by measuring the chord. The heavily cuticularized paired lateral pieces of the gubernaculum, which are equal in length and very prominent, have a characteristic shape with a denticle near the distal end. They are a little more than half the length of the longer spicule and the dorsally situated median plate of the gubernaculum is just a little longer than the lateral pieces (Text-figs. 24–25). In a larval male specimen (? 4th stage) the lateral pieces of the gubernaculum are of typical form, although the spicules are not fully developed.

FEMALE : Up to twelve eggs may be present in the uterus, their size varying from 90μ × 65μ—56μ × 55μ.

Discussion.

This species, which has not been described since de Man's paper (1886) has often been reported from the coasts of north west Europe where it appears to be very common. It has never been reported from the Mediterranean, and only Allgén has reported it from localities outside European waters. As is pointed out on page 185 only one of the seven new species described by Allgén can be considered valid and in view of the general uncertainty resulting from this assessment of his work it is better to consider the following records given by Allgén as doubtful : Falkland Is. (1959) ;

FIG. 15. *E. adriatica*. Lateral view of head. FIGS. 16–18 .*E. scampae*. Fig. 16. *En face* view of head. Fig. 17. Lateral view of head. Fig. 18. Ventral view of head. FIGS. 19–21. *E. shirleyae*. Fig. 19. *En face* view of head. Fig. 20. Lateral view of head. Fig. 21. Ventral view of head. (All to same scale.)

Hilo, Pacific Ocean (1951b) ; Tobago, West Indies (1947) (1 ♀); Bay of Panama ; Perlas Is. ; Taboguilla ; La Jolla shore, California (1947a).

Euchromadora striata (Eberth, 1863) Filipjev, 1918
(Text-figs. 26–27)

Odontobius striatus Eberth, 1863. *Untersuchungen über Nematoden.* Leipzig. 30, pl. 1, figs. 21–27.

Euchromadora striata, Filipjev, 1918. *Trav. Lab. Zool. Sebastopol* **2** (4), 241–244, pl. 7, fig. 47 ; Micoletzky, 1924. *S. B. Akad. Wiss. Wien* **133,** 155–157 ; Schuurmans Stekhoven, 1943. *Zool. Jb.* (*Syst. etc.*) **76,** 364–365, figs. 33 A–D ; Brunetti, 1952. *Monit. zool. ital.* **59,** 74–78, figs. 1 A, A^1, A^2, A^3; Wieser, 1954. *Hydrobiologia* **6,** 190–191, fig. 16.

nec *Euchromadora striata*, Chitwood, 1951. *Texas J. Sci.* **3,** 632, figs. 5 H–I (see p. 186).

TYPE LOCALITY : Nice, S. France.

MATERIAL STUDIED : 12 ♂♂ and 10 ♀♀ from the following localities (all among algae) : Covean, St. Agnes, Isles of Scilly, Sept., 1958 ; Hannafore, Looe, Cornwall (amongst *Furcellaria fastigiata*), E.L.W.S., June, 1956 ; Littlehampton, Sussex, August, 1959 (algae washed up on the shore) ; Skippers Island, Essex, February, 1961 ; Banyuls-sur-Mer, S. France, May, 1961. (B.M. (N.H.) Reg. Nos. 1963. 571–582).

	Body length (mm.)	Body ratios			
		a	*b*	*c*	length gubernaculum / length spicules × 100
Males	1·64	27·3	5·2	8·8	61·1
	1·77	25·3	5·0	8·7	51·8
	1·85	24·6	5·4	9·6	47·5
	2·00	24·7	5·6	8·3	55·9
	2·12	35·3	7·6	11·3	47·0
	2·16	28·8	5·7	9·8	43·5
	2·18	32·5	6·2	10·2	49·3
	2·20	23·9	5·8	11·0	53·5
	2·21	24·5	5·8	11·0	52·2
	2·23	27·9	5·9	10·1	54·9
	2·32	27·6	5·6	10·3	55·5
	2·64	31·0	6·4	11·7	48·9
					V
Females	1·97	24·6	5·5	8·5	50·7
	1·99	30·1	5·5	8·5	51·7
	2·26	25·1	5·9	9·5	50·4
	2·36	23·6	5·2	9·3	50·8
	2·52	22·9	6·3	9·0	49·6
	2·63	21·9	6·4	9·4	47·1
	2·76	22·1	6·2	8·9	50·0
	2·80	25·4	5·9	9·2	50·0
	2·90	26·3	6·9	11·6	48·3
	3·03	23·3	6·6	9·2	48·8

MEASUREMENTS (in mm. in order of body lengths). MALES. Body breadth : 0·060 ; 0·070 ; 0·075 ; 0·081 ; 0·060 ; 0·075 ; 0·067 ; 0·092 ; 0·090 ; 0·080 ; 0·084 ; 0·085. Head diameter : 0·030 ; 0·033 ; 0·030 ; 0·034 ; 0·033 ; 0·032 ; 0·030 ; 0·032 ; 0·032 ; 0·032 ; 0·033 ; 0·035. Length of oesophagus : 0·31 ; 0·35 ; 0·34 ; 0·36 ; 0·28 ; 0·38 ; 0·35 ; 0·38 ; 0·38 ; 0·38 ; 0·41 ; 0·41. Length of tail : 0·18 ; 0·20 ; 0·19 ; 0·24 ; 0·19 ; 0·22 ; 0·21 ; 0·20 ; 0·20 ; 0·22 ; 0·22 ; 0·22. Cloacal diameter : 0·044 ; 0·042 ; 0·051 ; 0·046 ; 0·042 ; 0·046 ; 0·040 ; 0·054 ; 0·055 ; 0·051 ; 0·054 ; 0·050. Length of spicules : 0·072 ; 0·085 ; 0·080 ; 0·084 ; 0·068 ; 0·085 ; 0·075 ; 0·086 ; 0·090 ; 0·082 ; 0·081 ; 0·092. Length of gubernaculum (lateral pieces) : 0·044 ; 0·044 ; 0·038 ; 0·047 ; 0·032 ; 0·037 ; 0·037 ; 0·046 ; 0·047 ; 0·045 ; 0·045 ; 0·045 ; 0·045.

FEMALES. Body breadth : 0·080 ; 0·066 ; 0·090 ; 0·100 ; 0·110 ; 0·120 ; 0·125 ; 0·110 ; 0·110 ; 0·130. Head diameter : 0·035 ; 0·036 ; 0·035 ; 0·038 ; 0·038 ; 0·037 ; 0·038 ; 0·040 ; 0·034 ; 0·038. Length of oesophagus : 0·36 ; 0·36 ; 0·38 ; 0·45 ; 0·40 ; 0·41 ; 0·44 ; 0·47 ; 0· 42; 0·46. Length of tail : 0·23 ; 0·23 ; 0·24 ; 0·25 ; 0·28 ; 0·28 ; 0·31 ; 0·30 ; 0·25 ; 0·33. Anal diameter : 0·043; 0·043 ; 0·045 ; 0·050 ; 0·050 ; 0·050 ; 0·050 ; 0·050 ; 0·044 ; 0·050. Distance of vulva from anterior end : 1·00 ; 1·03 ; 1·14 ; 1·20 ; 1·25 ; 1·25 ; 1·38 ; 1·40 ; 1·40 ; 1·48. Distance of nerve ring from anterior end : 0·165 (in specimen of 2·52 body length) ; 0·185 (in specimen of 3·03 body length). Distance of excretory pore from anterior end : 0·190 (in specimen of 2·52 body length) ; 0·208 (in specimen of 3·03 body length).

GEOGRAPHICAL DISTRIBUTION. FRANCE : Nice (Eberth, 1863) ; Banyuls-sur-Mer (Allgén, 1942 and present author, see above). ITALY : Isle of Ischia (Micoletzky, 1924) ; Gulf of Naples (Micoletzky, 1924 ; Brunetti, 1952 ; Wieser, 1954a) ; Portovenere (Wieser, 1954a) ; Sampiera, Sicily (Wieser, 1954a). OTHER MEDITERRANEAN LOCALITIES : Adriatic Sea (Micoletzky, 1924) ; Alexandria (Schuurman Stekhoven, 1943) ; Sea of Marmara (Prinkipo) (Micoletzky, 1924 ; Allgén, 1941) ; Black Sea (Sevastopol) (Filipjev, 1918) ; Suez (Micoletzky, 1924). South and east coast of ENGLAND ; Scilly Is. (present author, see above).

DISTINCTIVE CHARACTERS. Cuticle : 'Lateral plates' present. Cephalic setae : 12µ—15µ. Head and oesophagus : As in *E. vulgaris*.

MALE : The spicules are equal in length and identical in structure and in lateral view are quite stout. Eberth (1863), Filipjev (1918) and Brunetti (1952) figure this condition but Wieser (1954a) figures slender spicules. Some of the male specimens I have studied give the impression of slender spicules but, on closer examination, a weakly cuticularized ventral side could always be seen. Sometimes the appearance of slender spicules may be due to the angle from which they are studied. The lateral pieces of the gubernaculum are about half the length of the spicules and are of simpler form than those of *E. vulgaris* with no distinct denticle present near the distal end. This region, because it is a little ridged or thickened, sometimes gives the impression of a denticle. The proximal end does not widen as in *E. vulgaris* and is less prominent (Text-figs. 26 and 27).

FEMALE : Nineteen eggs have been seen in one specimen, but usually there are only about six in the uterus. Their size varies from about 50μ × 42μ—88μ × 50μ.

DISCUSSION. This species is very similar to *E. vulgaris*, but differs most decisively in the form of the spicules and gubernaculum. The most important character is the shape and length of the spicules. The length of the gubernaculum in proportion to the length of the spicules is usually about half, but sometimes a little greater.

E. striata has been reported frequently from the Mediterranean where it is probably very common. From my specimens it also appears to be common on the south coast of England, although not so common as *E. vulgaris* and *E. gaulica*. The two specimens (1♂ and 1♀ near together) found in a sample of algae from the Essex coast (Skippers Island) are the most northerly record for this species.

De Man (1886) recognizes that this species is similar to *E. vulgaris*, but without specimens he was unable to add anything to Eberth's description. In spite of Allgén (1942) Bastian (1865) did not report its occurrence on the coast of England, he merely repeats Eberth's diagnosis. As de Man (1886) mentions, Bastian did not recognize the similarity of *Odontobius striatus* to *Chromadora vulgaris*.

The description of *E. striata* by Chitwood (1951) from Aransas Bay, Texas is certainly not this species, but is closer to *E. gaulica*. The spicules, however, appear to be a little stouter than those of *E. gaulica*, according to Chitwood's figure, and the cephalic setae are shorter. It almost certainly represents a distinct species as will be dealt with later (see page 186).

Euchromadora gaulica Inglis, 1962

(Text-figs. 13–14, 22, 28–29)

Euchromadora gaulica Inglis, 1962. *Bull. Brit. Mus.* (*nat. Hist.*) (*Zool.*) **8** (5), 260–264, figs. 41–51 (♂♂ only, the ♀♀ belong to *E. striata* (Eberth, 1863)).

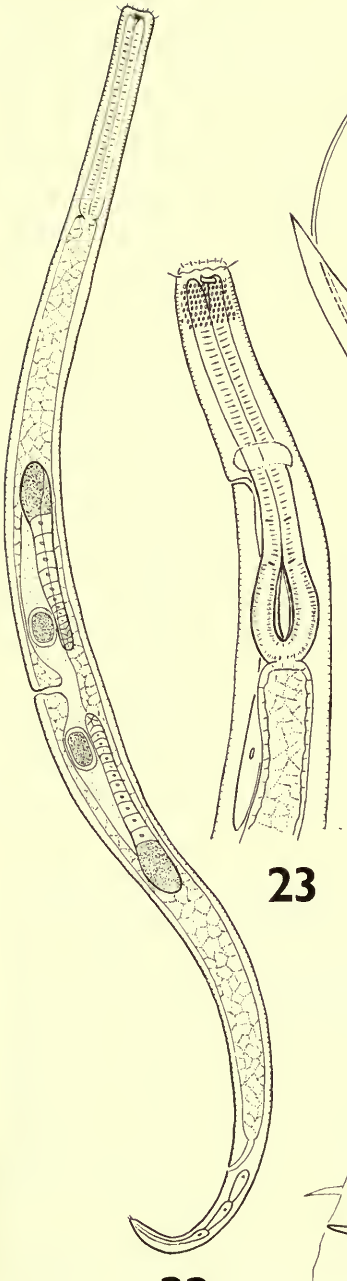
? *Euchromadora africana*, Schuurmans Stekhoven, 1950 (nec v. Linstow, 1908). *Mem. Inst. Sci. nat. Belg.* (2 ième Ser.) **37,** 137–138, figs. 81 A–D.

Euchromadora tridentata, Wieser, 1951 (nec Allgén, 1929). *Öst. zool. Z.* **3,** 455–456, figs. 6 a–c, e.

TYPE LOCALITY : Banyuls-sur-Mer, France.

MATERIAL STUDIED : Numerous specimens (12 ♂♂, 12 ♀♀, 4 larvae selected at random and measured). All among algae from the following localities : Croyde Bay, N. Devon (approx. M.L.W.S.), August, 1955 (the algae includes *Pelvetia canaliculata* unattached in a rock pool (B.M. Reg. Nos. 1956.8.16. 71–85) ; Wembury Bay, S. Devon (−0·2 ft. C.D.), June 1956 (Reg. Nos. 1963. 583–592) ; Littlehampton, Sussex (in algae washed up on the shore), August, 1959 (Reg. Nos. 1963. 593–595) ; Labrador Rock, near Teignmouth, S. Devon (in a fairly deep rock pool), July, 1961 (Reg. Nos. 1963. 596–600) ; Sprey Point, near Teignmouth, July, 1961 (Reg. Nos 1963. 611) ; Black Rock, Brighton, Sussex, June 1961 (Reg. No. 1963. 612) ; Banyuls-sur-Mer, S. France, May, 1961 (Reg. No. 1964. 152).

FIG. 22. *E. gaulica*. Showing the typical body form of the genus. FIG. 23. *E. adriatica*. Anterior end of body. FIGS. 24–25. *E. vulgaris*. Fig. 24. Lateral view of spicules and gubernaculum. Fig. 25. Ventral view of spicules and gubernaculum. FIGS. 26–27. *E. striata*: Fig. 26. Lateral view of spicules and gubernaculum. Fig. 27. Ventral view of spicules and gubernaculum. (24–27 to same scale.)



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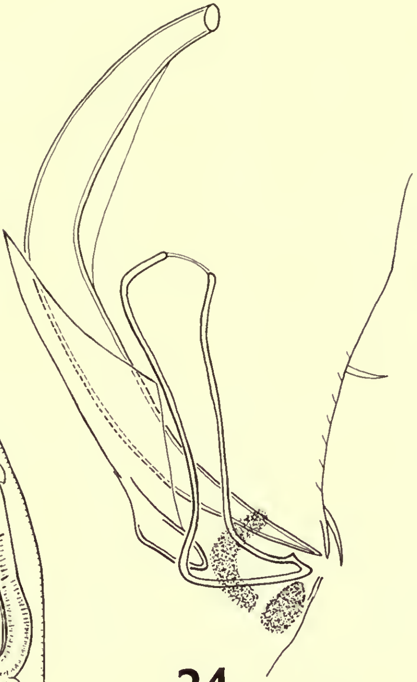

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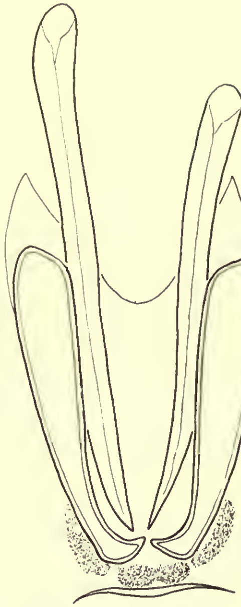

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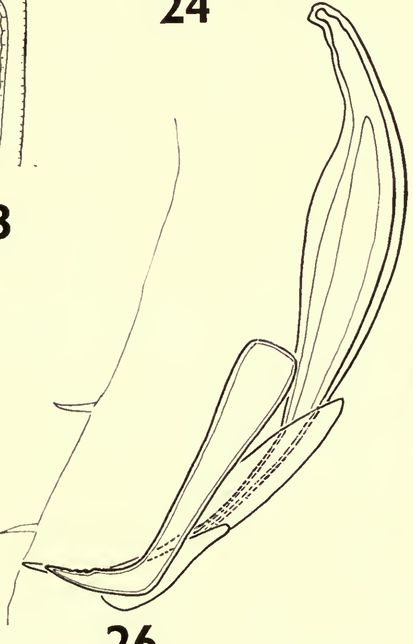

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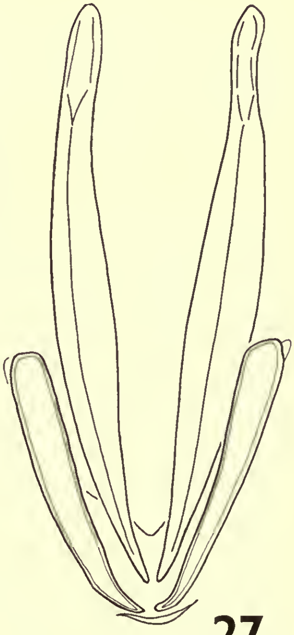

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		Body ratios			
	Body length (mm.)	*a*	*b*	*c*	$\frac{\text{length gubernaculum}}{\text{length spicules}} \times 100$
Males	1·18	31·1	5·6	7·9	61·4
	1·30	22·4	6·2	8·7	62·5
	1·42	29·5	6·0	8·3	55·1
	1·43	28·6	6·5	8·9	63·6
	1·44	28·8	6·8	8·5	57·8
	1·51	30·2	6·5	9·4	52·2
	1·53	27·8	6·9	9·0	63·8
	1·55	31·0	6·7	10·3	60·0
	1·60	26·7	6·1	9·4	61·7
	1·63	29·6	6·9	9·6	60·0
	1·67	30·4	6·9	9·8	64·0
	1·75	22·7	6·7	9·2	62·9
					V
Females	1·50	30·0	6·0	7·5	48·6
	1·53	25·5	6·4	8·0	49·7
	1·58	26·3	6·6	7·5	48·7
	1·65	28·9	6·1	8·7	50·9
	1·66	29·1	6·4	8·3	50·6
	1·72	24·5	6·6	7·8	49·4
	1·72	24·6	6·9	7·8	47·6
	1·74	20·4	6·7	8·7	49·4
	1·75	25·7	6·4	9·2	49·7
	1·75	25·0	6·5	7·9	48·5
	1·75	22·7	6·4	8·7	49·1
	1·77	24·5	6·8	7·7	48·6
Larvae	0·56	17·5	4·0	7·0	—
	0·76	20·5	4·5	6·3	—
	0·82	25·6	4·5	5·8	—
	0·83	20·7	4·6	6·4	48·2

MEASUREMENTS (in mm. in order of body lengths). MALES. Body breadth: 0·038; 0·058; 0·048; 0·050; 0·050; 0·050; 0·055; 0·050; 0·060; 0·055; 0·055; 0·077. Head diameter: 0·023 ; 0·025 ; 0·023 ; 0·022 ; 0·020 ; 0·020 ; 0·022 ; 0·023 ; 0·024 ; 0·022 ; 0·025 ; 0·026. Length of oesophagus : 0·21 ; 0·21 ; 0·22 ; 0·22 ; 0·21 ; 0·23 ; 0·22 ; 0·23 ; 0·26 ; 0·22 ; 0·24 ; 0·26. Length of tail : 0·15 ; 0·15 ; 0·17 ; 0·16 ; 0·17 ; 0·16 ; 0·17 ; 0·15 ; 0·17 ; 0·17 ; 0·17 ; 0·19. Cloacal diameter : 0·032 ; 0·040 ; 0·032 ; 0·030 ; 0·030 ; 0·030 ; 0·035 ; 0·030 ; 0·036 ; 0·030 ; 0·035 ; 0·037. Length of spicules : 0·044 ; 0·048 ; 0·049 ; 0·044 ; 0·045 ; 0·046 ; 0·047 ; 0·050 ; 0·047 ; 0·050 ; 0·050 ; 0·054. Length of gubernaculum (lateral pieces) : 0·027 ; 0·030 ; 0·027 ; 0·028 ; 0·026 ; 0·024 ; 0·030 ; 0·030 ; 0·029 ; 0·030 ; 0·032 ; 0·034.

FEMALES. Body breadth : 0·050 ; 0·060 ; 0·060 ; 0·057 ; 0·057 ; 0·070 ; 0·070 ; 0·085 ; 0·068 ; 0·070 ; 0·077 ; 0·072. Head diameter : 0·025 ; 0·025 ; 0·025 ; 0·027 ; 0·025 ; 0·025 ; 0·025 ; 0·025 ; 0·025 ; 0·025 ; 0·025 ; 0·025. Length of oesophagus : 0·25 ; 0·24 ; 0·24 ; 0·27 ; 0·26 ; 0·26 ; 0·25 ; 0·26 ;

0·27 ; 0·27 ; 0·27 ; 0·26. Length of tail : 0·20 ; 0·19 ; 0·21 ; 0·19 ; 0·20 ; 0·22 ; 0·22 ; 0·20 ; 0·19 ; 0·22 ; 0·20 ; 0·23. Anal diameter ; 0·035 ; 0·030 ; 0·032 ; 0·028 ; 0·031 ; 0·035 ; 0·032 ; 0·035 ; 0·032 ; 0·031 ; 0·033 ; 0·031. Distance of vulva from anterior end : 0·73 ; 0·76 ; 0·77 ; 0·84 ; 0·84 ; 0·85 ; 0·82 ; 0·86 ; 0·87 ; 0·85 ; 0·86 ; 0·86.

LARVAE. Body breadth : 0·032 ; 0·037 ; 0·032 ; 0·040. Head diameter : 0·022 ; 0·021 ; 0·022 ; 0·024. Length of oesophagus : 0·14 ; 0·17 ; 0·18 ; 0·18. Length of tail : 0·08 ; 0·12 ; 0·14 ; 0·13. Anal diameter : 0·022 ; 0·028 ; 0·028 ; 0·026.

Nerve ring observed in larva of body length 0·76 mm.–0·080 mm. from anterior end.

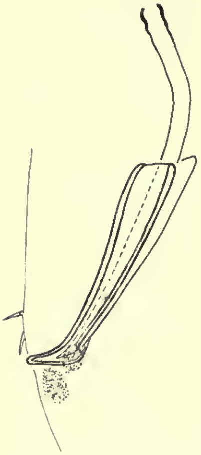
GEOGRAPHICAL DISTRIBUTION. MEDITERRANEAN SEA : Banyuls-sur-Mer (Inglis, 1962 and present author) ; Villefranche (Schuurmans Stekhoven, 1950). Coast of ENGLAND : Plymouth (Wieser, 1951, 1952) ; N. and S. coasts of Devon ; Brighton and Littlehampton, Sussex (present author, see above).

DISTINCTIVE CHARACTERS. Cuticle : ‘ Lateral plates ’ present. Cephalic setae : 10μ–12μ. Head and oesophagus : Similar to *E. vulgaris* and *E. striata* but smaller (Text-figs. 13 and 14). Excretory pore not seen, but a seta-like appendage is situated ventrally about 1·5 times the diameter of the head from the anterior end. Ventral gland large, situated at the anterior end of the intestine.

MALE : The spicules are slender, equal in length and identical in structure with a distinctive elbow-shaped curve towards the proximal end which is more marked in some specimens than in others. No tooth-like projection has been observed on the distal ends of the lateral pieces of the gubernaculum, which are more than half the length of the spicules (Text-figs. 28 and 29).

FEMALE: Up to five eggs have been seen at a time in the uterus. They vary in size from 35μ × 32μ–50μ × 45μ.

DISCUSSION. This species is similar to *E. vulgaris* and *E. striata* in the general form of the body and in the cuticularization of the onchial cavity, but is smaller and differs most decisively from the two former species in the form of the male genital apparatus. It is sometimes found in the same clump of algae with *E. striata,* which makes the separation of the females difficult. However, on the basis of size it appears possible to separate them. In mature female specimens (with eggs) of *E. gaulica* the head diameter does not exceed 27μ and the total length of the body is always less than 2 mm., while in mature females of *E. striata* the diameter of the head is always greater than 30μ and the total body length usually exceeds 2 mm. This separation of the two species is supported by the sample from Croyde Bay in which numerous specimens of *E. gaulica* (determined by males) are present, but no *E. striata* ; and of all those measured (gravid specimens) the female diameter never exceeds 27μ. This conclusion seems to be justified since the sexes are equally represented in large samples of species of *Euchromadora.*



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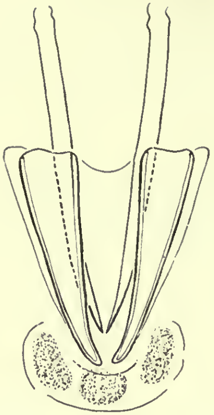

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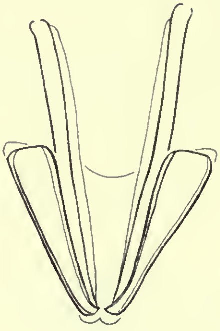

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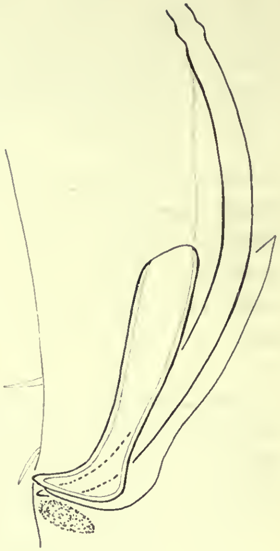

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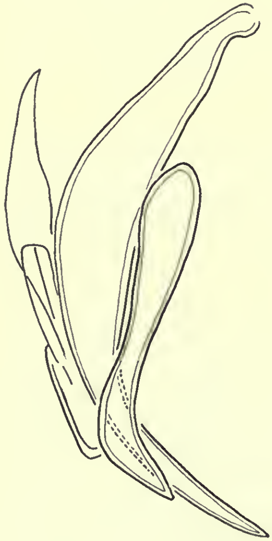

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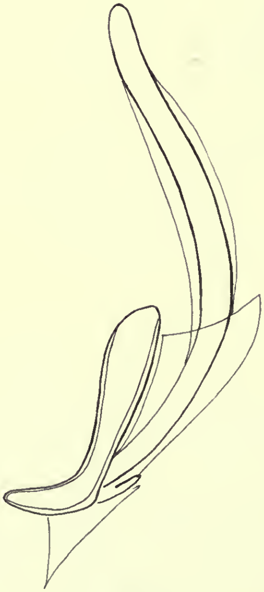

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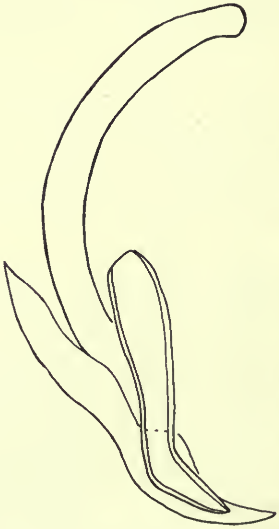

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FIGS. 28–29. *E. gaulica.* Fig. 28. Lateral view of spicules and gubernaculum. Fig. 29. Ventral view of spicules and gubernaculum. FIGS. 30–31. *E. adriatica.* Fig. 30. Ventral view of spicules and gubernaculum. Fig. 31. Lateral view of spicules and gubernaculum. FIG. 32. *E. loricata.* Lateral view of spicules and gubernaculum. FIG. 33. *E. scampae.* Lateral view of spicules and gubernaculum. FIG. 34. *E. shirleyae.* Lateral view of spicules and gubernaculum. (All to same scale, except Fig. 30.)

Inglis (1962) describes both males and females of *E. gaulica* but *E. striata* has since been found in the same locality (from a sample collected from almost the same locality) and as the diameter of the head of the females of *E. gaulica* examined by Inglis exceed 30µ it seems probable that his females really belong to *E. striata*.

Schuurmans Stekhoven's (1950) description of *E. africana* v. Linstow, 1908 from Villefranche is probably of *E. gaulica*, but there has been some confusion concerning the status of the former species. The original description of *E. africana* by v. Linstow (1908) is based on one female specimen from off the coast of south west Africa and the only thing that can be established from it with certainty is that it is a species of *Euchromadora*. Steiner (1918) redescribes what he considers to be this species (including ♂♂) from the west coast of Africa and states that the lateral pieces of the gubernaculum are half the length of the spicules, but does not figure nor give dimensions for the spicules and gubernaculum. Schuurmans Stekhoven (1950) also states the gubernaculum is half the length of the spicules based on his specimens from the Mediterranean (but in his figure the gubernaculum appears to be more than half the length of the spicules). On the basis of this Wieser (1954, 1955) uses the proportion gubernaculum half the length of the spicules, in conjunction with the total length of the spicules, as a key character for *E. africana*. However, it seems likely that v.Linstow, Steiner and Schuurmans Stekhoven were all dealing with different species and since none are described satisfactorily, I agree with Inglis (1962) that *E. africana* and all its records must be considered those of species dubiae.

From my studies of *E. gaulica*, where the length of the gubernaculum in proportion to the length of the spicules can vary from 52 to 65 per cent, it is clear that the use of this proportion must be applied with caution in separating species. The shape of the spicules and gubernaculum is much more important and useful, and where these structures are not figured or are figured inaccurately much confusion is likely to be caused.

Wieser (1951) describes what he considers to be *E. tridentata* Allgén, 1929 from Plymouth. He figures the spicules and gubernaculum and uses the fact that the gubernaculum is two-thirds the length of the spicules as a means of differentiating it from *E. striata* (where the gubernaculum is half the length of the spicules). The original description of *E. tridentata* Allgén, 1929 is based on only one immature specimen and could represent any similar form of *Euchromadora*. Wieser's specimens from Plymouth undoubtedly belong to *E. gaulica*.

E. tokiokai Wieser, 1955 from Japan is very similar to *E. gaulica* but the gubernaculum appears to be relatively longer. Although Wieser in his table gives its length as 66 per cent the length of the spicules, by his measurements and from his illustration it is about 75 per cent the length of the spicules. Also the tail of both sexes is shorter than in *E. gaulica*.

Euchromadora adriatica (v.Daday, 1901) Brunetti, 1952

(Text-figs. 3, 15, 23, 30–31)

Spilophora adriatica v. Daday, 1901. *Természetr. Füz.* **24,** 447–449, pl. 22, figs. 10–14, pl. 23, fig. 1.

Euchromadora adriatica, Brunetti, 1952. *Monit. zool. ital.* **59,** 80.
Euchromadora tyrrhenica Brunetti, 1952. *Monit zool. ital.* **59,** 73, 79–80, figs. 1 B, B¹, B².
Euchromadora tyrrenica, Inglis, 1962. *Bull. Brit. Mus. nat. Hist.* (*Zool.*) **8** (5), 264–266, figs. 52–56. (lapsus pro *tyrrhenica.*)

TYPE LOCALITY : Fiume, coast of Jugoslavia (Adriatic Sea).

MATERIAL STUDIED : 1 ♀ from Croyde Bay, N. Devon, August, 1955. (Brit. Mus. (N.H.) Reg. No. 1963. 606) ; 1 ♂ from a rock-pool, Labrador Rock, near Teignmouth, S. Devon, July, 1961 (Reg. No. 1963. 607) ; 2 ♂♂, 1 ♀ from a rock-pool (amongst *Cladophora* sp.), Wembury Bay, S. Devon, July, 1962 (Reg. Nos. 1963. 608–610). (All specimens were associated with algae.)

				Body ratios	
	Body length (mm.)	*a*	*b*	*c*	length gubernaculum / length spicules × 100
Males	1·24	22·5	5·4	8·8	63·1
	1·33	22·2	5·8	7·9	55·4
	1·73	19·6	6·8	8·6	60·8
					V
Females	1·70	17·0	5·7	8·9	48·2
	1·60	24·2	5·9	8·4	48·7

MEASUREMENTS (in mm. in order of body lengths). MALES. Body breadth: 0·055 ; 0·060 ; 0·088. Head diameter : 0·030 ; 0·028 ; 0·030. Length of oesophagus : 0·23 ; 0·23 ; 0·25. Length of tail : 0·14 ; 0·17 ; 0·19. Cloacal diameter : 0·035 ; 0·041 ; 0·058. Length of spicules ; 0·057 ; 0·065 ; 0·074. Length of gubernaculum (lateral pieces) : 0·036 ; 0·036 ; 0·045. Distance of nerve ring from anterior end : — ; 0·100 ; 0·115. Distance of excretory pore from anterior end : 0·115 ; 0·120 ; 0·135.

FEMALES. Body Breadth : 0·100 ; 0·066. Head diameter : 0·030 ; 0·031. Length of oesophagus : 0·30 ; 0·27. Length of Tail : 0·19 ; 0·19. Anal diameter : 0·057 ; 0·045. Distance of vulva from anterior end : 0·82 ; 0·78. Distance of nerve ring from anterior end : 0·130 ; 0·115. Distance of excretory pore from anterior end : 0·152 ; 0·135.

GEOGRAPHICAL DISTRIBUTION. ADRIATIC SEA : Fiume, coast of Jugoslavia (v.Daday, 1901) ; Rovinj, Istrien, Jugoslavia (Wieser, 1960). MEDITERRANEAN SEA : Gulf of Naples (Brunetti, 1952) ; Banyuls-sur-Mer (Inglis, 1962). ENGLAND: North and south coasts of Devon (present author, see above).

DISTINCTIVE CHARACTERS. Cuticle : ‘ Lateral plates ’ not seen in this species. Cephalic setae 10μ. Head and oesophagus : The dorsal onchium is more rectangular in outline than in any other species (Text-fig. 15). The double pointed enlarged subventral plates are not seen in this species. The oesophagus has a well defined posterior bulb and the excretory pore and ventral gland are fairly prominent (Text-fig. 23).

MALE : The spicules and gubernaculum are very similar to those of *E. gaulica*, but are somewhat longer and the spicules carry fine alae which are rather difficult to see and can be easily overlooked. The lateral pieces of the gubernaculum are about 60 per cent of the length of the spicules (Text-figs. 30 and 31).

FEMALE : Up to five eggs have been seen in the uterus. They measure 50μ × 40μ.

DISCUSSION. Micoletzky (1924) underrates the description of *Spilophora adriatica* by v.Daday (as in many other cases), stating that the posterior bulb of the oesophagus is shown too large. v.Daday's description and figures are adequate for the recognition of this species and, although he does not give the dimensions of the spicules, their length can be deduced fairly accurately from his figures, and they compare well with my specimens.

Brunetti (1952) recognizes *E. adriatica* but describes a very similar species (*E. tyrrhenica*) from the Tyrrhenian Sea. Since the descriptions of *E. tyrrhenica* by Brunetti (1952) and by Inglis (1962) do not differ from *E. adriatica* in any significant way, I consider *E. tyrrhenica* to be a synonym of *E. adriatica*. Dr. Inglis agrees with this synonymy.

Euchromadora loricata (Steiner, 1916) Steiner, 1918
(Text-fig. 32)

Spilophora loricata Steiner, 1916. *Zool. Jb.* (*Syst. etc.*) **39**, 526–532, pl. 19. figs. 3 a–n.
Euchromadora loricata, Steiner, 1918. *Zool. Anz.* **50**, 7.
nec *Euchromadora loricata*, Wieser, 1954. *Acta Univ. lund.* N.F. **50** (16), 104, figs. 152 a–b (=*E. archaica* Steiner & Hoeppli, 1926).

TYPE LOCALITY : Barents Sea.

MATERIAL STUDIED. 5 ♂♂, 3 ♀♀ from a sample of brown filamentous algae (*Chordaria flagelliformis*) from the coast of Spitzbergen, 1954 (B.M. (N.H.) Reg. Nos. 1963 601–605). More specimens were in the sample but in too poor condition to be of any use.

	Body length (mm.)	Body ratios			
		a	*b*	*c*	$\frac{\text{length gubernaculum}}{\text{length spicules}} \times 100$
Males	1·22	27·1	5·5	9·4	56·1
	1·23	28·6	5·8	10·2	61·8
	1·51	32·1	6·0	10·1	60·0
	1·62	32·4	6·0	10·1	61·8
	1·72	31·8	6·4	11·4	60·0
					V
Females	1·17	23·4	4·9	8·3	53·8
	1·50	25·0	6·2	9·4	50·0
	2·67	17·8	9·9	9·2	46·6

MEASUREMENTS (in mm. in order of body length). MALES. Body breadth : 0·045 ; 0·043 ; 0·047 ; 0·050 ; 0·054. Head diameter : 0·026 ; 0·025 ; 0·028 ; 0·027 ; 0·031. Length of oesophagus : 0·22 ; 0·21 ; 0·25 ; 0·27 ; 0·27 . Length of tail : 0·13 ; 0·12 ; 0·15 ; 0·16 ; 0·15. Cloacal diameter : 0·045 ; 0·040 ; 0·047; 0·050 ; 0·054. Length of spicules : 0·066 ; 0·055 ; 0·070 ; 0·068 ; 0·070. Length of gubernaculum (lateral pieces) : 0·037 ; 0·034 ; 0·042 ; 0·042 ; 0·042. Distance of nerve ring from anterior end : 0·141 (in specimen of 1·23 body length). Distance of excretory pore from anterior end : 0·150 (in specimen of 1·23 body length).

FEMALES. Body breadth : 0·050 ; 0·060 ; 0·150. Head diameter : 0·028 ; 0·030 ; 0·030. Length of oesophagus : 0·24 ; 0·24 ; 0·27. Length of tail : 0·14 ; 0·16 ; 0·29. Anal diameter : 0·040 ; 0·048 ; 0·050. Distance of vulva from anterior end : 0·63 ; 0·75 ; 1·25. Distance of nerve ring from anterior end : 0·100 ; 0·110 ; 0·120. Distance of excretory pore from anterior end : 0·120 ; — ; 0·148.

GEOGRAPHICAL DISTRIBUTION. Barents Sea (Steiner, 1916) ; Coast of Spitzbergen (present author, see above).

DISTINCTIVE CHARACTERS. Cuticle : ' Lateral plates ' present. Cephalic setae : 11µ—13µ. Head and oesophagus : Similar to *E. adriatica*, oesophagus with a distinct posterior bulb ; excretory pore and ventral gland quite prominent.

MALE : The spicules are fairly stout and without alae. The lateral pieces of the gubernaculum are more than half the length of the spicules (Text-fig. 32).

FEMALE : Two eggs seen in one large specimen, measuring 50µ × 35µ.

DISCUSSION. Although only a few of the specimens from Spitzbergen are in good condition, they compare well with Steiner's original description. This species differs from *E. adriatica* chiefly in the form of the spicules, which are stout in comparison and without alae. Other differences are the occurrence of ' lateral plates ' in the cuticle and the length of the cephalic setae, which are a little longer in this species.

Wieser's (1954) description of *E. loricata* from Chile does not refer to this species, but is similar to *E. archaica* Steiner and Hoeppli, 1926.

Allgén reports *E. loricata* from the west coast of Sweden (1951, 1953) but, as Wieser (1954) points out, these specimens do not have a definite posterior bulb to the oesophagus and the species cannot be recognised by the shape of the tail alone as Allgén claims. For this reason the following reports by Allgén must also be considered very doubtful : La Jolla, California (1947a) ; Bay of Panama (1951b) ; Port Jackson, Australia (1951b) ; Tasmania (1927) ; Hilo, Pacific Ocean (1951b) ; South Georgia (1959).

Euchromadora scampae sp. nov.
(Text-figs. 16–18, 33)

TYPE LOCALITY : Croyde Bay, N. Devon.

MATERIAL STUDIED : 12 ♂♂, 7 ♀♀, 3 larvae from the following localities (all among algae): Croyde Bay, N. Devon (among *Pelvetia canaliculata* and other algae unattached in a rock-pool, approx. M.L.W.S.), August, 1955 (B.M. (N.H.) Reg. Nos.

1963. 622–625 (No. 624 selected as holotype)) ; Putsborough, nr. Woolacombe, N. Devon, August, 1955 (Reg. Nos. 1963. 626–627) ; Poyllbrein, south coast, Isle of Man (approx. M.L.W.S.), August, 1961 (Reg. Nos. 1963. 613–621) ; Wembury Bay, S. Devon (among *Cladophora* sp.), July, 1962 (Reg. Nos. 1963, 628–629).

		Body ratios			
	Body length (mm.)	*a*	*b*	*c*	length gubernaculum / length spicules × 100
Males	1·32	34·7	6·0	8·2	54·5
	1·60	35·5	5·9	8·4	48·4 (Holotype)
	1·67	37·9	6·2	9·3	54·0
	1·73	38·4	7·4	7·5	50·0
	1·75	38·9	7·5	9·7	60·0
	1·76	39·1	7·8	10·0	56·6
	1·78	33·6	7·0	8·9	53·3
	1·78	34·2	7·7	9·6	45·2
	1·90	38·0	7·6	—	53·6
	1·90	38·0	8·2	10·5	55·2
	1·96	34·4	7·3	10·3	52·4
	2·04	35·8	7·5	9·3	63·1
					V
Females	1·57	39·2	6·0	7·2	49·0
	1·63	37·9	6·4	7·7	—
	1·90	36·5	—	8·6	49·5
	1·91	32·9	7·1	8·5	49·7
	1·98	27·5	7·6	8·4	48·5
	2·01	28·7	7·4	8·0	51·2
	2·07	29·6	7·7	9·8	50·2
Larvae	0·64	21·3	4·0	6·7	(? 1st or 2nd stage)
	0·84	28·0	4·2	6·8	(?2nd stage)
	1·00	31·2	4·8	6·6	(? 3rd stage)

MEASUREMENTS (in mm. in order of body lengths). MALES. Body breadth : 0·038 ; 0·045 ; 0·044 ; 0·045 ; 0·045 ; 0·045 ; 0·053 ; 0·052 ; 0·050 ; 0·050 ; 0·057 ; 0·057. Head diameter : 0·020 ; 0·022 ; 0·021 ; 0·023 ; 0·020 ; 0·025 ; 0·020 ; 0·021 ; 0·021 ; 0·019 ; 0·020 ; 0·021. Length of oesophagus : 0·22 ; 0·27 ; 0·27 ; 0·23 ; 0·23 ; 0·22 ; 0·25 ; 0·23 ; 0·25 ; 0·23 ; 0·27 ; 0·27. Length of tail : 0·16 ; 0·19 ; 0·18 ; 0·23 ; 0·18 ; 0·17 ; 0·20 ; 0·18 ; — ; 0·18 ; 0·19 ; 0·22. Cloacal diameter : 0·036 ; 0·045 ; 0·040 ; 0·045 ; 0·040 ; 0·045 ; 0·045 ; 0·047 ; 0·045 ; 0·046 ; 0·050 ; 0·050. Length of spicules : 0·055 ; 0·062 ; 0·050 ; 0·060 ; 0·050 ; 0·053 ; 0·060 ; 0·062 ; 0·056 ; 0·058 ; 0·057 ; 0·057. Length of gubernaculum (lateral pieces) : 0·030 ; 0·030 ; 0·027 ; 0·030 ; 0·030 ; 0·030 ; 0·032 ; 0·028 ; 0·030 ; 0·032 ; 0·030 ; 0·036. Distance of nerve ring from anterior end : 0·085 in specimen of 1·75 body length ; 0·112 in specimen of 1·96 body length. Distance of excretory pore from anterior end : 0·115 in specimen of 1·96 body length.

FEMALES. Body breadth : 0·040 ; 0·043 ; 0·052 ; 0·058 ; 0·072 ; 0·070 ; 0·070. Head diameter : 0·021 ; 0·022 ; 0·021 ; 0·020 ; 0·021 : 0·022 : 0·022. Length of oesophagus : 0·26 ; 0·25 ; — ; 0·27 ; 0·26 ; 0·27 ; 0·27. Length of tail : 0·22 ; 0·21 ; 0·22 ; 0·22 ; 0·23 ; 0·25 ; 0·21. Anal diameter : 0·035 ; 0·030 ; 0·030 ; 0·032 ; 0·035 ; 0·042 ; 0·035. Distance of vulva from anterior end : 0·77 ; — ; 0·94 ; 0·95 ; 0·96 ; 1·03 ; 1·04.

LARVAE. Body breadth : 0·030 ; 0·030 ; 0·032. Head diameter : 0·020 ; 0·020 ; 0·022. Length of oesophagus ; 0·16 ; 0·19 ; 0·21. Length of tail : 0·096 ; 0·124 ; 0·152. Anal diameter : 0·024 ; 0·025 ; 0·025.

GEOGRAPHICAL DISTRIBUTION. Coasts of North and South Devon ; Isle of Man (present author, see above).

DISTINCTIVE CHARACTERS. Cuticle : The punctation markings at the anterior end are oval shaped and only a little smaller than the remaining rows of hexagonal markings which commence just posterior to the onchial cavity. Structures comparable to the ‘ lateral plates ’ occur as shown in Text-fig. 5, not always distinct. Cephalic setae : 8µ. Head and oesophagus : The dorsal onchium is fairly small and the onchial cavity is simple with two simple, tooth-like projections, situated subventrally (Text-figs. 16–18). The oesophagus broadens very gradually towards the posterior end which is without a distinct bulb. The excretory pore and ventral gland are indistinct.

MALE : The spicules are bow-shaped and alate, equal in length and identical in structure. The lateral pieces of the gubernaculum are very similar in shape to those of *E. gaulica* and are only a little more than half the length of the spicules. The two pre-cloacal setae are very small and not easily seen (Text-fig. 33).

FEMALE : Up to six eggs at a time seen in the uterus. Their size varying from 50µ × 30µ–55µ × 35µ.

DISCUSSION. This species is most like *E. amokurae* and *E. mediterranea* in the simple form of the head, but differs from the first in lacking a posterior bulb to the oesophagus and in not having a knob-like swelling on the proximal end of the spicules. It differs from the second, *E. mediterranea*, in which the spicules which are longer and lack alae, and the gubernaculum is relatively smaller in *E. scampae*.

Euchromadora shirleyae sp. nov.

(Text-figs. 2, 8, 19–21, 34)

TYPE LOCALITY : Off the coast of South Africa.

MATERIAL STUDIED : Numerous specimens (12 ♂♂, 12 ♀♀, 2 larvae selected at random and measured) from coarse white sand at a depth of 27 metres, 32° 02′ S./18° 17′ E. on 2.7.61. (University of Capetown Ecological Survey Reference No. WCD.91. (B.M. (N.H.) Reg. Nos. 1963. 939–1,060). Ref. No. WCD.99 (Reg. Nos. 1963. 1,061–1,072.)

		Body ratios			
	Body length (mm.)	*a*	*b*	*c*	length gubernaculum / length spicules × 100
Males	3·12	52·0	8·2	12·0	56·2
	3·20	53·3	7·4	12·3	58·3
	3·20	49·2	8·4	11·8	49·1
	3·25	46·4	7·7	13·0	55·9
	3·29	49·8	7·8	12·2	62·1
	3·35	51·5	7·9	11·9	57·1
	3·40	48·6	8·5	13·1	58·5
	3·50	56·4	7·8	12·5	53·7
	3·54	54·5	9·6	13·1	55·9
	3·85	53·5	8·2	12·0	58·8
	4·05	57·8	9·0	11·9	56·2 (Holotype)
	4·12	56·4	8·6	12·5	58·5
					V
Females	3·02	37·7	7·5	9·1	46·3
	3·15	42·0	7·7	8·7	47·6
	3·15	37·9	7·5	9·5	47·6
	3·20	45·7	7·1	7·4	46·9
	3·20	42·7	8·0	8·6	46·9
	3·32	38·2	6·9	8·3	45·8
	3·38	38·4	7·5	9·6	47·3
	3·48	41·9	7·4	8·3	43·4
	3·50	38·9	7·4	8·5	48·6
	3·62	44·7	7·5	8·6	46·9
	3·63	45·4	7·6	9·3	46·8
	3·80	47·5	7·9	9·5	47·4
Larvae	1·68	37·3	5·6	9·3	(larval ♂, gubernaculum seen)
	2·25	44·1	6·0	9·8	(? 4th stage ♂)

MEASUREMENTS (in mm. in order of body lengths). MALES. Body breadth : 0·060 ; 0·060 ; 0·065 ; 0·070 ; 0·066 ; 0·065 ; 0·070 ; 0·062 ; 0·065 ; 0·072 ; 0·070 ; 0·073. Head diameter : 0·027 ; 0·029 ; 0·027 ; 0·028 ; 0·028 ; 0·027 ; 0·028 ; 0·028 ; 0·028 ; 0·030 ; 0·030 ; 0·030. Length of oesophagus : 0·38 ; 0·43 ; 0·38 ; 0·42 ; 0·42 ; 0·42 ; 0·40 ; 0·45 ; 0·37 ; 0·47 ; 0·45 ; 0·45. Length of tail : 0·26 ; 0·26 ; 0·27 ; 0·25 ; 0·27 ; 0·28 ; 0·26 ; 0·28 ; 0·27 ; 0·32 ; 0·34 ; 0·33. Cloacal diameter : 0·060 ; 0·060 ; 0·055 ; 0·062 ; 0·056 ; 0·060 ; 0·060 ; 0·060 ; 0·065 ; 0·070 ; 0·065 ; 0·068. Length of spicules : 0·064 ; 0·060 ; 0·057 ; 0·068 ; 0·066 ; 0·070 ; 0·065 ; 0·067 ; 0·068 ; 0·068 ; 0·073 ; 0·065. Length of gubernaculum (lateral pieces) : 0·036 ; 0·035 ; 0·028 ; 0·038 ; 0·041 ; 0·040 ; 0·038 ; 0·036 ; 0·038 ; 0·040 ; 0·041 ; 0·038.

FEMALES. Body breadth.: 0·080 ; 0·075 ; 0·083 ; 0·070 ; 0·075 ; 0·087 ; 0·088 ; 0·083 ; 0·090 ; 0·081 ; 0·080 ; 0·080. Head diameter : 0·030 ; 0·026 ; 0·027 ; 0·030 ; 0·028 ; 0·030 ; 0·027 ; 0·030 ; 0·030 ; 0·029 ; 0·030 ; 0·030. Length of oseophagus : 0·40 ; 0·41 ; 0·42 ; 0·45 ; 0·40 ; 0·48 ; 0·45 ; 0·47 ;

0·47 ; 0·48 ; 0·48 ; 0·48. Length of tail : 0·33 ; 0·36 ; 0·33 ; 0·43 ; 0·37 ; 0·40 ; 0·35 ; 0·42 ; 0·41 ; 0·42 ; 0·39 ; 0·40. Anal diameter : 0·045 ; 0·047 ; 0·050 ; 0·049 ; 0·050 ; 0·050 ; 0·050 ; 0·050 ; 0·050 ; 0·050 ; 0·050 ; 0·050. Distance of vulva from anterior end : 1·40 ; 1·50 ; 1·50 ; 1·50 ; 1·50 ; 1·52 ; 1·60 ; 1·50 ; 1·50 ; 1·70 ; 1·70 ; 1·80.

LARVAE. Body breadth : 0·045 ; 0·051. Head diameter : 0·026 ; 0·026. Length of oesophagus : 0·30 ; 0·37. Length of tail : 0·18 ; 0·23. Anal diameter : 0·040 ; 0·048.

GEOGRAPHICAL DISTRIBUTION. Coast of South Africa. (Present author.)

DISTINCTIVE CHARACTERS. Cuticle : The punctation markings are always hexagonal to rectangular in shape and not oval. The arrangement of the markings on the dorsal and ventral surfaces is unique. The hexagonal markings between the two clear zones (as described on page 161) continue throughout the length of the worm. However, on the ventral surface they become narrower in the region of the cloaca or anus (see Text-fig. 8). 'Lateral plates' not seen. Body setae absent, but this may be due (as explained on page 161) to the method of fixation. Cephalic setae : 6µ–7µ. Head and oesophagus : The inner circle of six labial papillae is typical but the intermediate circle of sense organs is modified as setae, which are about the same length as the four cephalic setae, i.e. 6µ–7µ (Text-fig. 19). The dorsal onchium is fairly large, but the onchial cavity is weakly sclerotized compared with the other larger species, and two simple ventro-lateral onchia are present (see Text-figs. 19–21). The nerve ring is difficult to see and the excretory pore and ventral gland have not been seen.

MALE : The spicules are equal in length and identical in structure, bow-shaped and non-alate. The gubernaculum is usually a little more than half their length (Text-fig. 34). There are no pre-cloacal setae as there are in all the other species studied by me. Instead there are two papillae (Text-fig. 8), which can only be seen in ventral view, in the same position. These are of quite different form from the sucker-like supplements (which can usually be seen easily in a lateral view) commonly found on other Chromadoridae.

FEMALE : The vulva is a relatively prominent longitudinal slit, in contrast to the transverse slit in other species (Text-figs. 2 and 4). No eggs have been seen.

DISCUSSION. This species differs from all the others in a number of ways, particularly in the form and arrangement of the cephalic papillae, the punctations of the cuticle, the shape of the vulva and the long slim body. All the other species studied are littoral forms while *E. shirleyae* is from much deeper waters.

REVIEW OF THE REMAINING SPECIES

Currently the genus *Euchromadora* contains twenty eight nominal species of which I accept only fifteen, seven of which are described above. This assessment is based largely on the form of the oesophagus and the male genital apparatus in conjunction with the general body form. Although the structure of the head does supply useful additional characters the inadequate nature of most of the available descriptions makes their use impossible.

Of seven species described by Allgén only one can be considered valid, because of his very inadequate descriptions and poor figures. It is unlikely that specimens belonging to these nominal species could ever be recognized. For this reason most of the geographical records of Allgén must be considered doubtful, especially as he reports the occurrence of some European species in the southern hemisphere. As Wieser (1954) points out it is not possible to differentiate species by the shape of the tail as Allgén claims. Some of the earlier inadequate descriptions, although by reliable workers, are due to an insufficient understanding of the characters important in differentiating species. Thus, Steiner (1918), for example, describes six species from the west coast of Africa which cannot be recognized as he does not figure, nor give dimensions of, the spicules and gubernaculum, although males were present in most cases.

Euchromadora africana v. Linstow, 1908 species dubia

Euchromadora africana v. Linstow, 1908. *Denkschr. Med. nat. Ges. Jena* **13,** 28, pl. IV, figs. 20–21.
?*Euchromadora africana,* Steiner, 1918. *Zool. Anz.* **50,** 8–10, fig. 1.
nec *Euchromadora africana* of Schuurmans Stekhoven, 1950 (= *? E. gaulica* Inglis, 1962).

TYPE LOCALITY : Luederitzbucht, South West Africa.

GEOGRAPHICAL DISTRIBUTION. Coast of South West Africa (v.Linstow, 1908) ; Lome, Togo, west coast of Africa ; Teneriffa (Steiner, 1918).

The status of this species is discussed on page 177 where it is regarded as a species dubia.

Euchromadora amokurae (Ditlevsen, 1921) Allgén, 1929

Spilophora amokurae Ditlevsen, 1921. *Vidensk. Medd. naturh. Foren. Kbh.* **73,** 16–17, fig. 11, pl. I, fig. 6, pl. II, figs. 4, 5 ; Allgén, 1928. *Nyt. Mag. for Naturw.* **66,** 251–253, figs. 1 a–b
Euchromadora amokurae, Allgén, 1929. *Zool. Anz.* **84,** 137–140 ; Wieser, 1954. *Acta Univ. lund. N.F.* **50** (16), 105–106, figs. 154 a–g.

TYPE LOCALITY : Auckland I., North arm of Carnley harbour.

GEOGRAPHICAL DISTRIBUTION. Auckland I. (Ditlevsen, 1921) ; Campbell I. (Allgén, 1928) ; Macquarie I. (Allgén, 1929a) ; I. de los Estados (Staten I.) off Tierra del Fuego (Allgén, 1930, 1959) ; Cape Brett, New Zealand (Ditlevsen, 1930) ; San Pedro, California (Allgén, 1947a) ; Honolulu ; Zamboanga, Philippine Is. ; Port Jackson, Australia ; Bay of Panama ; La Jolla shore, California (Allgén, 1951b) ; Chile (Gerlach, 1953a) (Wieser, 1954) ; Falkland Is. ; South Georgia ; Graham Land (Allgén, 1959). Japan (Wieser, 1955).

This species, which is similar to *E. scampae* in the form of the head, appears to be common in the southern hemisphere. It is characterized by a knob-like swelling at the proximal end of the spicules, and the oesophagus has a posterior bulb.

Euchromadora archaica Steiner and Hoeppli, 1926

Euchromadora archaica Steiner & Hoeppli, 1926. *Arch. Schiffs. Tropenhyg.* **30,** 558–565, 571–573, figs. L–P.
Euchromadora loricata of Wieser, 1954. *Acta Univ. lund.* N.F. **50** (16), 104, figs. 152 a–b. (nec Steiner, 1916.)

TYPE LOCALITY : Shore of Joshi Island, near Kobe, Japan.

GEOGRAPHICAL DISTRIBUTION. Joshi I., Japan (Steiner and Hoeppli, 1926) ; Coast of Chile (Wieser, 1954).

This species which has a well defined posterior oesophageal bulb is similar to *E. adriatica*, but is a larger form. It is also similar to *E. loricata* (Steiner, 1916), but differs from it chiefly in the form of the spicules, which are slender, and in the absence of ' lateral plates '. This latter character is particularly stressed by Steiner and Hoeppli.

Euchromadora chitwoodi nom. nov.

Euchromadora striata of Chitwood, 1951. *Texas J. Sci.* **3,** 632, figs. 5 H–I. (nec Eberth, 1863.)

TYPE LOCALITY: Mud Island, Aransas Bay, Texas.

GEOGRAPHICAL DISTRIBUTION. Aransas Bay, Texas (Chitwood, 1951).

This species is similar to *E. gaulica*, but the spicules are a little stouter, the gubernaculum is about half the length of the spicules and the cephalic setae are shorter. See further discussion under *E. striata* (page 172).

Euchromadora denticulata Cobb, 1914 species dubia

Euchromadora denticulata Cobb, 1914. *Contr. Sci. Nematology* **1,** 8, 1 fig.

TYPE LOCALITY : Cape Royds, Antarctic.

GEOGRAPHICAL DISTRIBUTION. Cape Royds, Antarctic (Cobb, 1914).

Because no males were present and the description is insufficient I consider this to be a species dubia.

Euchromadora dubia Steiner, 1918 species dubia

Euchromadora dubia Steiner, 1918. *Zool. Anz.* **50,** 10–11, fig. 2.

TYPE LOCALITY : Luederitzbucht, coast of South West Africa.

GEOGRAPHICAL DISTRIBUTION. Luederitzbucht, coast of South West Africa Steiner, 1918).

This species, which has fairly long cephalic setae and a posterior bulb to the oesophagus, is unlikely to be recognized, as the male genital apparatus is not figured nor are dimensions given for these structures. It is therefore treated as a species dubia.

Euchromadora elegans Allgén, 1947 species dubia

Euchromadora elegans Allgén, 1947. *Vidensk. Medd. naturh. Foren.* **110,** 159–160, figs. 56 a–c.

TYPE LOCALITY: La Jolla shore, California.

GEOGRAPHICAL DISTRIBUTION. Coast of California (Allgén, 1947a).

In spite of an adequate number of specimens (incl. 18 ♂♂) the resulting description is so very poor that it can only be treated as that of a species dubia.

Euchromadora eumeca Steiner, 1918 species dubia

Euchromadora eumeca Steiner, 1918. *Zool. Anz.* **50,** 14–15, fig. 5.

TYPE LOCALITY: Porto Seguro, Senegal.

GEOGRAPHICAL DISTRIBUTION. Senegal, West Africa (Steiner, 1918).

There is no adequate description of the male genital apparatus and as a result this form is unlikely to be recognized and is better treated as a species dubia.

Euchromadora hupferi Steiner, 1918. species inquirenda

Euchromadora (*Odontocricus*) *hupferi* Steiner, 1918. *Zool. Anz.* **50,** 13–14, fig. 4.

TYPE LOCALITY: Gorée in Senegal.

GEOGRAPHICAL DISTRIBUTION. Senegal, West Africa (Steiner, 1918).

As the markings on the cuticle of this species are quite different to those of all other species of *Euchromadora,* Steiner referred it to a new subgenus *Odontocricus,* which Filipjev (1934) apparently regards as a distinct genus. Since the description is poor and inadequate ; without illustrations of the male genital apparatus or head and only a sketch of the general appearance of the cuticle ; this species will be treated as a species inquirenda since we can hope the characteristic cuticular pattern will enable it to be recognized in future.

Euchromadora inflatispiculum Schuurmans Stekhoven, 1943

Euchromadora inflatispiculum Schuurmans Stekhoven, 1943. *Zool. Jb.* (*Syst. etc.*) **76,** 365–366, figs. 34 A–D ; 1950. *Mem. Inst. Sci. nat. Belg.* (2 ième Ser.) **37,** 139, figs. 82 A–D.

TYPE LOCALITY: Villefranche, Mediterranean Sea.

GEOGRAPHICAL DISTRIBUTION. MEDITERRANEAN SEA : Villefranche ; Alexandria (Schuurmans Stekhoven, 1943, 1950).

This species is very characteristic in lacking lateral pieces to the gubernaculum and by the shape of the slender spicules which are swollen at their distal ends. Schuurmans Stekhoven's illustration in the 1950 description shows the spicules as being much shorter than the one given in his 1943 paper. The onchial cavity appears to be of intermediate complexity. Until more specimens are found nothing more can be added to the rather unsatisfactory descriptions by Schuurmans Stekhoven.

Euchromadora kryptospiculum (Allgén, 1942) Allgen, 1951 species dubia

Spilophora kryptospiculum Allgén, 1942. *Zool. Jb.* (*Syst. etc.*) **76,** 49–50, figs. 11 a–c.
Euchromadora kryptospiculum, Allgén, 1951. *Vidensk. Medd. naturh. Foren. Kbh.* **113,** 390–391, figs. 54 a–c.

TYPE LOCALITY : Banyuls-sur-Mer, S. France.

GEOGRAPHICAL DISTRIBUTION. MEDITERRANEAN SEA: Banyuls-sur-Mer (Allgén, 1942). CALIFORNIA : La Jolla shore, (Allgén, 1951b).

This species is very poorly described and, as Wieser (1954) has pointed out, the two descriptions of Allgén most probably represent different forms. From the figures of the male it seems that the spicules and gubernaculum are not fully developed, and that Allgén has been dealing with immature forms. This species must be treated as a species dubia.

Euchromadora linstowi Allgén, 1959 species dubia

Euchromadora linstowi Allgén, 1959. *Freeliving Nematodes. Further Zoological Results of the Swedish Antarctic Expedition* 1901–1903, Stockholm, 137–138.
Euchromadora sp. v. Linstow, 1892. *Mitt. naturh. Mus. Hamburg* **9,** 65.

TYPE LOCALITY : South Georgia.

GEOGRAPHICAL DISTRIBUTION. South Georgia (v.Linstow, 1892 ; Allgén, 1959) ; Falkland Islands (Allgén, 1959).

As the description of this species is, like all the descriptions in this publication, inadequate it must be treated as a species dubia.

Euchromadora lüderitzi Steiner, 1918 species dubia

Euchromadora lüderitzi Steiner, 1918. *Zool. Anz.* **50,** 12–13, fig. 3.

TYPE LOCALITY : Luederitzbucht, South West Africa.

GEOGRAPHICAL DISTRIBUTION. Coast of South West Africa (Steiner, 1918).

Although males are present Steiner does not figure nor give dimensions of the spicules and gubernaculum. As this species is unlikely to be recognized it must be treated as a species dubia.

Euchromadora mediterranea Allgén, 1942

Euchromadora mediterranea Allgén, 1942. *Zool. Jb.* (*Syst. etc.*) **76,** 51–52, figs. 12 a–c ; Wieser, 1954. *Hydrobiologia* **6,** 189–190, figs. 15 a–c.

TYPE LOCALITY : Banyuls-sur-Mer, S. France.

GEOGRAPHICAL DISTRIBUTION. MEDITERRANEAN SEA: Banyuls-sur-Mer (Allgén, 1942) ; Italy : Portovenere ; Sorrento, Gulf of Naples (Wieser, 1954a).

This species, which is very similar to *E. scampae* in the form of the head, is characterized by slender spicules and the large, very prominent lateral pieces of the gubernaculum, which are quite stout and whose extremities (especially the proximal ends) are more rounded than in *E. scampae.*

Euchromadora meridiana Cobb, 1914 species dubia

Euchromadora meridiana Cobb, 1914. *Contr. Sci. Nematology* **1,** 8, 9, 28, 1 fig.

TYPE LOCALITY : Cape Royds, Antarctic.

GEOGRAPHICAL DISTRIBUTION. Cape Royds, Antarctic (Cobb, 1914).

The description of this species is so inadequate that it is unlikely to be recognized and is best treated as a species dubia.

Euchromadora mortenseni (Allgén, 1947) Wieser, 1954 species dubia

Spilophora mortenseni Allgén, 1947. *Vidensk. Medd. naturh. Foren. Kbh.* **110,** 56–57, figs. 6 a–c.
Euchromadora mortenseni, Wieser, 1954. *Acta Univ. lund.* N.F. **50** (16), 103.

TYPE LOCALITY : Tobago, West Indies.

GEOGRAPHICAL DISTRIBUTION. Tobago, West Indies (Allgén, 1947).

In spite of a very large number of specimens Allgén's description of this species is totally inadequate and it can only be considered a species dubia.

Euchromadora parafricana Gerlach, 1958

Euchromadora parafricana Gerlach, 1958. *Kieler Meeresforsch.* **14,** 245–246, pl. 41, figs. 4 a–f.

TYPE LOCALITY : Insel Sarso, Red Sea.

GEOGRAPHICAL DISTRIBUTION. Red Sea (Gerlach, 1958).

This species is very distinct in the form of the punctation pattern of the cuticle, particularly on the head region. The usual small anterior punctations are not followed by large blocks as in other species. Instead posterior to them are five rows of oval-shaped punctations, then five rows of circular, and then a more typical pattern of large blocks continues over the remainder of the body.

Euchromadora permutabilis Wieser, 1954

Euchromadora permutabilis Wieser, 1954. *Acta Univ. lund.* N.F. **50** (16), 104–105, figs. 153 a–f

TYPE LOCALITY : Coast of Chile.

GEOGRAPHICAL DISTRIBUTION. Coast of Chile (Wieser, 1954).

This is a fairly large species, the females attaining a length of 3·14 mm. and the males 2·98 mm. The spicules and gubernaculum are similar in shape to *E. striata* but are much longer (104μ–133μ). The lateral pieces of the gubernaculum are just a little more than half the length of the spicules. In head and general form it is also similar to *E. striata,* but the tail is much shorter.

Euchromadora stateni Allgén, 1930 species dubia

Euchromadora stateni Allgén, 1930. *Zool. Anz.* **90,** 32–34, figs. 4 a–b.

TYPE LOCALITY : I. de los Estadod (Staten I.) off Tierra del Fuego, South America.

GEOGRAPHICAL DISTRIBUTION. Tierra del Fuego Archipelago, South America (Allgén, 1930).

This species is based on one immature specimen only and is unlikely to be recognized from the poor description. This species must therefore be regarded as a species dubia.

Euchromadora tokiokai Wieser, 1955

Euchromadora tokiokai Wieser, 1955. *Publ. Seto mar. biol. Lab.* **4,** 173, figs. 8 a–c.

TYPE LOCALITY : Below the Seto Marine Biological Laboratory, Shirahama-tyô, Wakayama-ken, South of Osaka, on the western coast of Kii Peninsula, near Sionomisaki, Japan.

GEOGRAPHICAL DISTRIBUTION. Western coast of Kii Peninsula, Japan (Wieser, 1955) ; Red Sea (Gerlach, 1958).

This species is very similar to *E. gaulica*, but differs from it in the greater length of the gubernaculum and in the shorter tail. In this species the lateral pieces of the gubernaculum are about 75 per cent of the spicules.

Euchromadora tridentata Allgén, 1929 species dubia

Euchromadora tridentata Allgén, 1929. *Capita zool.* **2** (8), 35, figs. 11 a–c.
nec *Euchromadora tridentata* of Wieser, 1951 (=*E. gaulica* Inglis, 1962).

TYPE LOCALITY : Kristineberg, west coast of Sweden.

GEOGRAPHICAL DISTRIBUTION. West coast of Sweden (Allgén, 1929).

This species is based only on one immature specimen. Schuurmans Stekhoven (1935) suggests that it may be the larva of *E. vulgaris* or *E. loricata*. However, as this cannot be established with certainty it is better treated as a species dubia.

Euchromadora tyrrhenica Brunetti, 1952

=*E. adriatica* (v. Daday, 1901) (see page 177).

LIST OF SPECIES OF *EUCHROMADORA* CONSIDERED VALID

E. vulgaris (Bastian, 1865) de Man, 1886 [Type species].
E. adriatica (v.Daday, 1901) Brunetti, 1952
E. amokurae (Ditlevsen, 1921) Allgén, 1929.
E. archaica Steiner and Hoeppli, 1926.
E. chitwoodi nom. nov.[=*E. striata* of Chitwood, 1951].

E. gaulica Inglis, 1962.
E. inflatispiculum Schuurmans Stekhoven, 1943.
E. loricata (Steiner, 1916) Steiner, 1918.
E. mediterranea Allgén, 1942.
E. parafricana Gerlach, 1958
E. permutabilis Wieser, 1954.
E. scampae sp. nov.
E. shirleyae sp. nov.
E. striata (Eberth, 1863) Filipjev, 1918.
E. tokiokai Wieser, 1955.

LIST OF NOMENCLATORIAL CHANGES PROPOSED

E. denticulata Cobb, 1914=species dubia.
E. dubia Steiner, 1918=species dubia.
E. elegans Allgén, 1947=species dubia.
E. eumecea Steiner, 1918=species dubia.
E. (*Odontocricus*) *hupferi* Steiner, 1918=species inquirenda.
E. kryptospiculum (Allgén, 1942) Allgén, 1951=species dubia.
E. linstowi Allgén, 1959=species dubia.
E. loricata of Allgén, 1927 ; 1947a ; 1951b ; 1959=species dubiae.
E. loricata of Wieser, 1954=*E. archaica* Steiner & Hoeppli, 1926.
E. lüderitzi Steiner, 1918=species dubia.
E. meridiana Cobb, 1914=species dubia.
E. mortenseni (Allgén, 1947) Wieser, 1954=species dubia.
E. stateni Allgén, 1930=species dubia.
E. striata of Chitwood, 1951=*E. chitwoodi* nom. nov.
E. tridentata Allgén, 1929=species dubia.
E. tridentata of Wieser, 1951=*E. gaulica* Inglis, 1962.
E. tyrrhenica Brunetti, 1952=*E. adriatica* (v.Daday, 1901) Brunetti, 1952.
E. vulgaris of Allgén, 1947 ; 1947a ; 1951b ; 1959=species dubiae.

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NATURAL HIST

WILLIAM G. FRY

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ZOOLOGY Vol. 12 No. 6
LONDON: 1965

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1 JUN 1965

BY

WILLIAM G. FRY
British Museum (Natural History)

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THE FEEDING MECHANISMS AND PREFERRED FOODS OF THREE SPECIES OF PYCNOGONIDA

By WILLIAM G. FRY

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SYNOPSIS

Laboratory experiments demonstrate that *Austrodecus glaciale* and *Rhynchothorax australis*, inhabiting the same Antarctic benthic environment, have highly specific and different food preferences. The structures of the proboscides and cephalic somites of the two species are adapted to these food preferences. *A. glaciale* is the first pycnogonid shown to feed on Polyzoa, while *Rh. australis* is adapted to feed on hydroid polyps. *Pycnogonum stearnsi*, from the north-eastern Pacific littoral, which feeds on Actinian tissue, is morphologically very similar to *Rh. australis*. The disposition of proboscis nerves and muscles in the three species is quite different from anything hitherto described in the Pycnogonida. In previous descriptions basal circular muscles have been interpreted as nerve rings. This prevented, up to now, the proposal of a mechanically reasonable interpretation of the functioning of the proboscis.

INTRODUCTION

LARGE areas of the sea bottom in McMurdo Sound (Ross Sea, Antarctica) are covered with a dense mat of sponge spicules. Within and on this mat occur large numbers of coelenterates, polyzoans, echinoderms, sponges, lamellibranchs and polychaetes, and the interstices of the mat are largely filled with flocculent detritus. Bullivant (1959b, 1961) has published excellent photographs of this kind of environment.

Amongst other forms also present in varying abundance in this mat are several species of Pycnogonida, of which the most abundant appear to be *Austrodecus glaciale* Hodgson (s.s. Stock 1957) and *Rhynchothorax australis* Hodgson. Since the size ranges of these two species are very similar (Text-fig. 1), and since they were found in the same hauls on a number of occasions, it appears unlikely that they exploit equally all the aspects of their common environment.

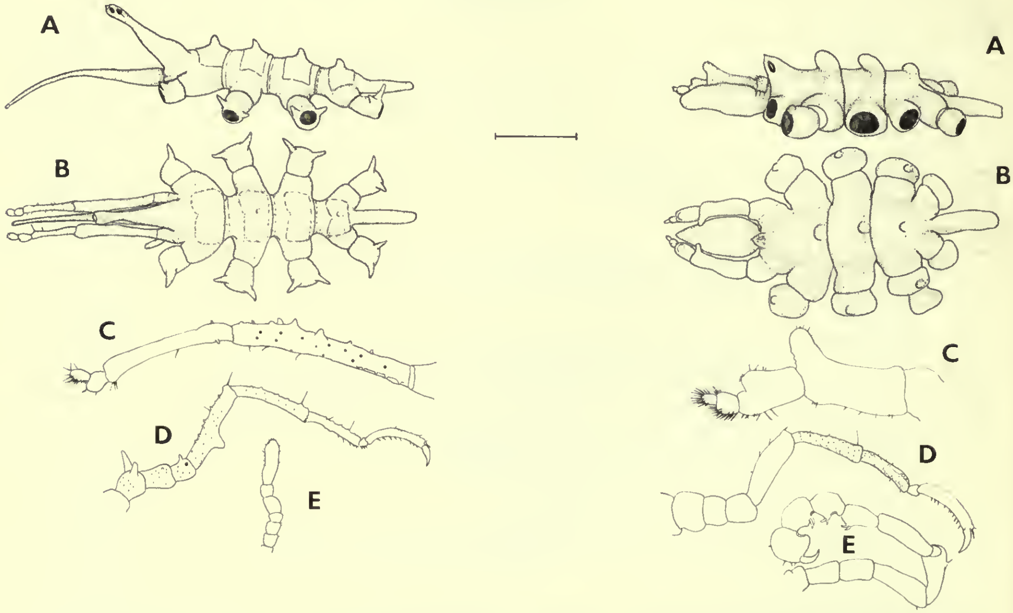

FIG. 1. Left : *Austrodecus glaciale* Hodgson. Right : *Rhynchothorax australis* Hodgson. A, view from left side ; B, dorsal view ; C, left palp ; D, 3rd left leg ; E, left oviger. A, B, and D to the scale indicated (1 mm.) ; C and E further enlarged.

During the austral summer of 1961/62, while the author was at the Naval Air Facility Base at McMurdo Sound, an attempt was made to determine the food preferences of *A. glaciale* and *Rh. australis* by studying their behaviour in an artificial environment in the laboratory. The observed differences in food preferences were sufficiently striking to warrant a detailed investigation of the morphology of the two species. The morphological differences between the two species are very marked, but since both species are adapted for life in a probably unique type of environment, it was felt advisable also to investigate the morphology of a species representative of a more ubiquitous environment.

Pycnogonum stearnsi Ives was available to the author in large numbers and was selected for comparison with the two Antarctic species. This species belongs to a genus with representatives in the littoral zone of most regions of the world. The available information suggests that the preferred foods of all the species of the genus are various species of anthozoans. The faunal associations of *P. stearnsi* are—for a pycnogonid—very well documented.

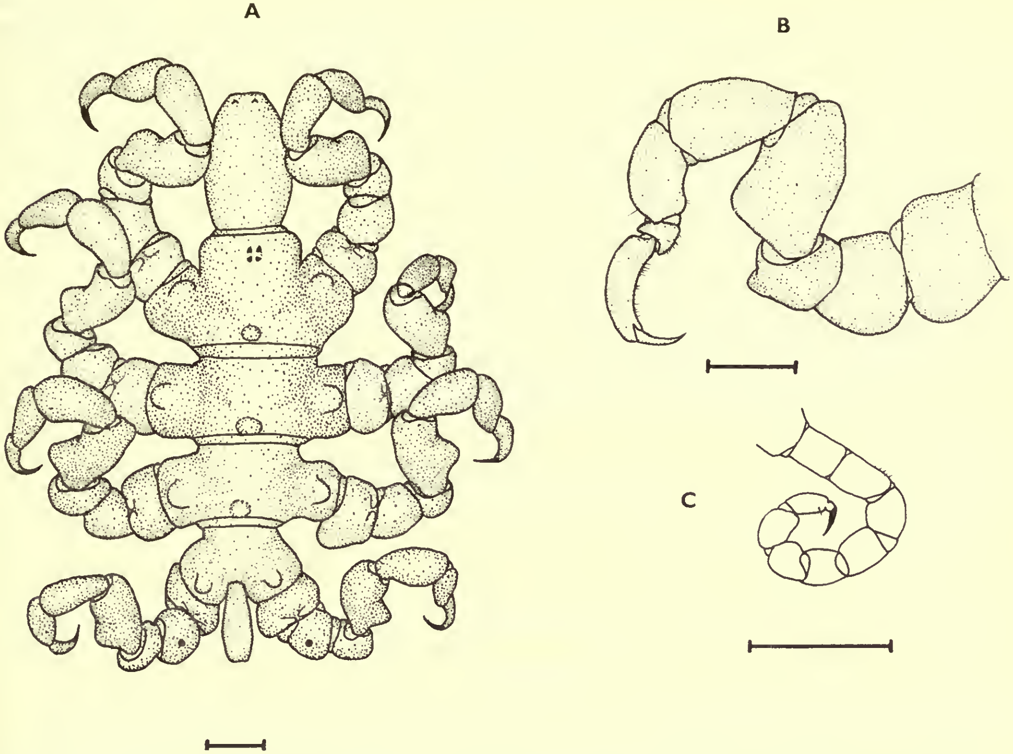

FIG. 2. *Pycnogonum stearnsi* Ives. A, dorsal view ; B, 3rd left leg ; C, left oviger of male. The scales represent 1 mm.

THE FEEDING PREFERENCES OF *AUSTRODECUS GLACIALE* AND *RHYNCHOTHORAX AUSTRALIS*

Material

The specimens of Pycnogonida, together with other organisms and substrate from their immediate environment, were collected with modified Petersen and orange-peel grabs worked through the ice-holes maintained by the Stanford University laboratory personnel. *A. glaciale* and *Rh. australis* proved to be most plentiful under Ice Hole No. 3, situated at 77° 59′ 5″ S., 166° 44′ 3″ E., in approximately 280 metres of water. The Pycnogonida retained for observation and subsequent histological work were all taken at this station during November.

Potential food organisms were selected from the samples which contained specimens of the two species of pycnogonids. The range of potential food was further narrowed, to what appeared to be sixteen species, by the selection of only those kinds of material on which pycnogonids had been observed during the sorting of the contents of 24 grab hauls from Ice Hole No. 3. Subsequent systematic evaluation revealed that in fact 18 species of Coelenterata, Polyzoa, Tunicata, and Porifera were used in the study. Table 1 lists the taxa and the symbols by which they are referred to below.

TABLE I

Taxonomic status of the sixteen kinds of potential food material presented to *Rhynchothorax australis* and *Austrodecus glaciale*.

Coelenterates.
  Eudendrium tottoni Stechow = Hy 1.[1]
  Symplectoscyphus epizooticus Totton = Hy 2.
  Symplectoscyphus vanhoeffeni Totton = Hy 3.
  Thouarella variabilis Wright & Studer = Hy 4.
  Alcyonium paessleri May = Hy 5.
  Hydrodendron arborea (Allman) = Hy 6.
Polyzoa.
  Cellarinella laytoni Rogick = Br 1.
  Escharoides bubeccata Rogick + *Notoplites drygalski* (Kluge) = Br 2.
  Cellarinella foveolata (Waters)[2] = Br 3.
  Camptoplites bicornis (Busk) var. *magna* (Kluge) + *Cellaria wandeli* Calvet = Br 4.
  Cellaria vitrimuralis Rogick + *C. moniliorata* Rogick = Br 5.
Tunicate.
  Unidentified = Tu 1.
Porifera.
  Suberites sp. = Sp 1.
  Cinachyra barbata Sollas = Sp 3.
  Tedania sp. = Sp 4.
  Suberites sp. = Sp 7 (= Sp 1).

[1] The letters and numbers after the names correspond to the potential food materials listed in Tables II and III.

[2] Possibly a synonym of both *C. roydsi* Rogick and *C. rossi* Rogick.

Maintenance of the Organisms

Grab contents were sorted in the laboratory, in trays jacketed with fresh snow, and the pycnogonids and potential food materials were placed in shallow jars of fresh sea water at —1·8°C. The jars were kept in a large cooling unit. During fifteen sets of observations, the water temperature was observed to fluctuate between —0·5 and —1·8°C. The organisms appeared unaffected by these fluctuations. The pycnogonids remained active throughout the whole period of study, and the coelenterates maintained rapid reactions to gentle probing.

The sea water in the jars was replaced with equal quantities of fresh sea water every 48 hours, and the potential food organisms were replaced with freshly collected material every 96 hours.

The Pycnogonida were segregated according to species, and each jar of pycnogonids contained fragments of each of the sixteen kinds of food material. Care was taken to ensure that the quantities of each of the potential food materials in each jar were as nearly equal as possible. When several very small fragments of any one kind of food material were required to make up the correct total bulk of that material, the small fragments were placed together. It was hoped that these precautions would ensure that the chances of a pycnogonid encountering any one kind of food material, during random locomotion, would be equal for all the kinds of food material.

An additional precaution taken was to ensure that only potential food material which was mostly or entirely composed of live tissues was presented to the pycnogonids.

Observations

Observations were made over a period of nine days, at eight or twelve hour intervals. A count was made, at each set of observations, of the number of specimens of each species of pycnogonid on each kind of potential food material. During the periods of observation, the jars of organisms were kept jacketed in fresh snow, and studied with the aid of a binocular microscope. Great care was taken to avoid disturbing the contents of the jars while the counts were made.

Specimens of *Rh. australis* were seen to ingest polyps of *Eudendrium tottoni* but ingestion of food by *A. glaciale* was never observed. However, a check was made, at each set of observations, on the degree of distension of the gut in all of the pycnogonids. This is readily done as, during life, both species of pycnogonid are sufficiently transparent for the gut to be visible. Throughout the nine days of observations all the pycnogonids maintained full, or partially full, gut diverticula.

Data

The results of observations on seventeen specimens of *Rh. australis* and five specimens of *A. glaciale* are shown in Table II and III.

TABLE II

The observed frequencies of occurrence of five adult specimens of *Austrodecus glaciale* Hodgson on sixteen kinds of potential food material during a period of nine days.

	1st Presentation		*2nd Presentation*		*Total*	
	f	%f	f	%f	f	%f
Hy 1	4	13·76	1	3·44	5	8·60
Hy 2	2	6·88	2	6·88	4	6·88
Hy 3	1	3·44	0	0·0	1	3·72
Hy 4	0	0·0	0	0·0	0	0·0
Hy 5	0	0·0	0	0·0	0	0·0
Hy 6	0	0·0	1	3·44	1	1·72
Br 1	1	3·44	1	3·44	2	3·44
Br 2	2	6·88	3	10·32	5	8·60
Br 3	8	27·52	10	34·40	18	30·96
Br 4	4	13·76	1	3·44	5	8·60
Br 5	0	0·0	1	3·44	1	1·72
Tu 1	0	0·0	1	3·44	1	1·72
Sp 1	0	0·0	0	0·0	0	0·0
Sp 3	3	10·32	4	13·76	7	12·04
Sp 4	3	10·32	0	0·0	3	5·16
Sp 7	1	3·44	4	13·76	5	8·60
Totals	29		29		58	

TABLE III

The observed frequencies of occurrence of seventeen adult specimens of *Rhynchothorax australis* Hodgson on sixteen kinds of potential food material during a period of nine days.

	1st Presentation		*2nd Presentation*		*Total*	
	f	%f	f	%f	f	%f
Hy 1	42	45·78	15	15·75	57	30·76
Hy 2	3	3·27	6	6·30	9	4·78
Hy 3	0	0·0	7	7·35	7	3·67
Hy 4	2	2·18	7	7·35	9	4·76
Hy 5	0	0·0	4	4·20	4	2·10
Hy 6	0	0·0	5	5·25	5	2·62
Br 1	0	0·0	4	4·20	4	2·10
Br 2	3	3·27	8	8·40	11	5·83
Br 3	6	6·54	4	4·20	10	5·37
Br 4	1	1·09	5	5·25	6	3·17
Br 5	3	3·27	5	5·25	8	4·26
Tu 1	0	0·0	1	1·05	1	0·52
Sp 1	13	14·27	2	2·10	15	8·28
Sp 3	7	7·63	3	3·15	10	5·39
Sp 4	5	5·25	15	15·75	20	10·60
Sp 7	6	6·54	4	4·20	10	5·37
Totals	91		95		186	

These data were analysed by means of the χ^2 test, in order to ascertain how far the segregation of the pycnogonids on the potential food organisms differed from situations due entirely to chance wandering. The null hypothesis proposed for the χ^2 test was that the pycnogonids had no preference for any particular kind of animal substrate, and that they would therefore be expected to distribute themselves equally among the sixteen kinds of potential food material. This hypotheses was strongly discredited for both *Rh. australis* and *A. glaciale*, since for both sets of data $P = \geqslant 0{\cdot}001$.

From this result of χ^2 tests it is clear that, within the experimental environments at least, *Rh. australis* has a strong preference for association with the hydroid *Eudendrium tottoni* Stechow (= Hy 1), and that *A. glaciale* has a strong preference for association with the polyzoan *Cellarinella foveolata* (Waters) (=Br 3). In the case of both pycnogonids these major preferences appear to be three times as strong as the animals' preference for association with any other kind of potential food.

Although details of the feeding mechanisms of the two species of pycnogonid and the morphologies of the preferred food substances strongly suggest that the calculated preferences are strongly associated with quite different feeding mechanisms (see below), the effect of a large part of the experimental environment cannot be determined accurately. This is the free space in the experimental containers.

Both *A. glaciale* and *Rh. australis* show very marked thigmotropism when disturbed. Individuals will cling tightly together if placed in water on a bare smooth surface. The high percentage of total occurrences on potential food materials and the corresponding low percentage of occurrences free in the containers is probably a good indication of the strength of this thigmotropism.

Frequencies on Food Materials	*Rhynchothorax*	*Austrodecus*
Total Possible	216 = 100%	64 = 100%
Total Observed	186 = 85·96%	58 = 90·59%

It is quite possible that thigmotropism induced artificially high frequencies of occurrences on all the potential food materials, since the experimental substrate—smooth floored glass jars—was very far removed in texture from the pycnogonids' natural substrate of sponge spicules, hydroids, flocculent detritus, etc.

The total of 10–15% of non-occurrences on potential food substances indicates that thigmotropism was not the only factor controlling the distribution of the pycnogonids within the jars.

THE FOOD PREFERENCES OF PYCNOGONUM STEARNSI

The faunal associations of this species are so well documented (Hedgpeth 1951, Ricketts & Calvin 1963, Zeigler 1960), and apparently so consistent, that no experimental determination of food preferences seems necessary. *P. stearnsi* occurs in the mid-tide and low-tide horizons of the littoral zone along the western coast of North America from Alaska to Southern California (Hedgpeth 1961). It has been found closely associated with hydroids (e.g. *Aglaophenia* spp.), the tunicate *Clavelina huntsmani*, and, by far the most frequently, with the anemones *Anthopleura xanthogrammica* (Brandt) and *Bunodactis elegantissima* (Brandt).* The pycnogonids are frequently found clustered around the bases of the anemones, with their proboscides clearly inserted into the anemones' tissues. The author has found immature nematocysts amongst the gut contents of specimens of *P. stearnsi*, freshly collected from round the bases of both species of anemone. There can thus be little doubt that the anemones form an important part of the food of this species.

THE MORPHOLOGY OF THE PROBOSCIS IN THE THREE SPECIES

Methods

All specimens of the three species were treated in the same fashion, preparatory to examination. Before fixing in Bouin's solution, the specimens were narcotised, by adding ethyl acetate to the water in which they were resting. It was hoped that this would bring about the relaxation of all muscles. Immersion of active pycnogonids in formalin or alcohol frequently results in violent spasmodic movements, and the animals may remain in spasm until the tissues are fixed. The possibility that muscles may be found in a state of violent, abnormal, contraction, renders even more difficult than usual the interpretation of mechanical systems by means of serial sections alone.

Prior to sectioning, the animals† were immersed in formal formic acid. Without this precaution, even if specimens are mounted in ester-wax for sectioning, it is very difficult to obtain whole sections. The pycnogonid cuticle is not only very thick, but very brittle. Even following immersion in the acid solution and sectioning in ester-wax, it was not possible to obtain entire sections thinner than 10μ, and to obtain useful sections of the largest specimens of *P. stearnsi* it was necessary to treat them with diaphanol.

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*It appears likely that these two anemones are but form varieties of a single species.

†B.M. (N.H.) Regn. Nos. 1963.6.27.1–5 and 1964.1.13.1–4.

All sections were stained with Mallory's triple stain. This stain was selected because its effects on cuticle with different mechanical properties appear to be remarkably constant. There is striking similarity in the distribution of stain colours in the cuticles of young and old specimens of all three species. The distribution of colours in the stained cuticles of the three species of pycnogonids is quite reconcilable with the associations of colour and mechanical properties described by Manton (1958, pp. 548–550).

The extrinsic musculature of the proboscis.

In outward appearance the pycnogonid proboscis is a simple tube, which varies in its external diameter at different points along its length. Morphological studies show clearly that the underlying plan of symmetry of the proboscis is triradial, and this is in fact suggested in external appearance by the presence of three lip lobes.

Seen in cross-section, the proboscis appears to have been formed by the fusion of a single dorsal and two ventrolateral antimeres. (See Text-figs. 6 and 7, Pl. 3–5.) Embryological studies, culminating in the recent publication by Sanchez(1959), indicate that the dorsal antimere is an outgrowth from a " cephalic " somite, while the two ventrolateral antimeres arise from a slightly more posterior somite. Some circumstantial evidence in support of this explanation of the origin of the ventrolateral antimeres occurs in the genera *Phoxichilidium* and *Anoplodactylus*, in which the proboscis frequently bears a pair of ventrolateral protuberances. These outgrowths indicate that the somite giving rise to the ventrolateral antimeres of the proboscis may, in the past, have borne a pair of ventral appendages.*

While the intrinsic musculature, the gut configuration, and the nervous system of the proboscis are clearly based on a triradial plan of symmetry, the muscles causing the entire proboscis to move are not disposed triradially. The extrinsic muscles consist of at least two pairs of major muscles, which may be subdivided to some extent, and one smaller pair of ventral muscles which are variably present.

One of the major pairs of muscles retracts the dorsal proximal end of the proboscis. This pair of muscles is referred to here as the " M 1 muscles " (Text-figs. 3, 4 and 5, Pl. 1. M 1). The other major pair of muscles retracts the ventral proximal end of the proboscis. This pair is referred to here as the " M 2 muscles " (Text-figs. 3, 4 and 5, Pl. 1. M 2), while the " M 3 muscles " (Text-fig. 3, M 3) are the smaller muscles which appear to be partly ancillary in function to the M 2 muscles. Other muscle pairs not directly concerned in the movements of the proboscis are referred to as " M 4 ", " M 5 " (Text-figs. 3, 4 and 5).

In *Rhynchothorax australis* (Text-fig. 3) three pairs of extrinsic muscles appear to be concerned in movements of the proboscis.

The muscles of the pair M 1 have their origins, on a transverse dorsal apophysis

*Stock (1963) has described a new species, *Anoplodactylus unilobus*, in which the proboscis bears a single ventral outgrowth.

(Ap 1), medial to the origins of the M 2 muscles. The M 1 muscles pass forward between the dorsal ganglion and the dorsal surface of the gut, within the circumoesophageal commissure, and insert on the anterior dorsal surface of the arthrodial membrane between the proboscis and the cephalic somite. In their passage forward, the two muscles converge, so that they are inserted on the arthrodial membrane more closely than they originate on the wall of the cephalic somite.

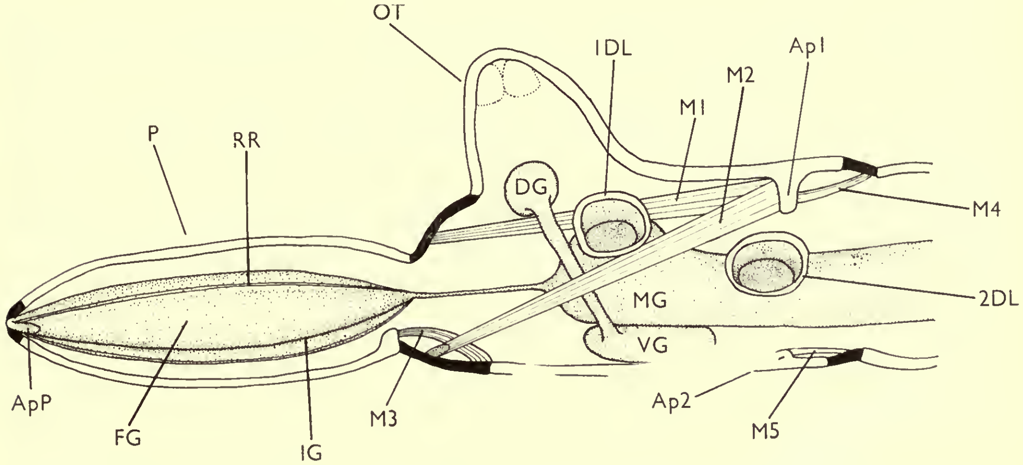

FIG. 3. Proboscis and cephalic somite of *Rh. australis* seen in diagrammatic longitudinal optical section. Unsclerotized arthrodial membrane is shown as solid black. Only the structures of the left side are shown. See p. 223 for the key to the lettering.

The M 2 muscles have their origins, on the same dorsal transverse apophysis (Ap 1), lateral to the origins of the M 1 muscles. They pass forward and downward, outside the circumoesophageal commissure, and are inserted on the ventrolateral walls of the arthrodial membrane between proboscis and cephalic somite. In their forward passage the two muscles of the pair diverge slightly.

The M 3 muscles are very much shorter and less stout than either the M 1 or the M 2 muscles. They have their origins on the proximal ventral portion of the arthrodial membrane between proboscis and cephalic somite, and their insertions on a low apophysis on the ventral proximal edge of the proboscis wall.

In this species, as in the other two studied, there are no visible antagonists to these sets of muscles, and it is reasonable to suppose that the fluid body contents are the antagonists of all the extrinsic proboscis muscles.

Accepting this hypothesis, and using it to interpret the mechanics of proboscis movement, it may be said that, during life the system is in balance when all the extrinsic muscles have slight tonus, and the proboscis is held with its longitudinal axis roughly parallel to the longitudinal axis of the body. When the M 1 muscles contract, the proximal dorsal surface of the proboscis will be pulled back and the dorsal portion of the arthrodial membrane will buckle inwards. The whole proboscis will tilt about an axis at the line of folding in the arthrodial membrane and in this way the distal end of the proboscis will be raised slightly.

When the M 2 muscles contract the ventral proximal edge of the proboscis will be pulled backwards and upwards. The net effect of this movement will be a lowering of the distal end of the proboscis.

The angles which the M 1 and M 2 muscles make with the longitudinal axes of the body and proboscis suggest that the M 2 muscles will produce a much greater movement from the balanced state than will the M 1 muscles.

It appears that the M 1 muscles have three functions. When acting by themselves, they will assist the hydrostatic pressure in returning the system to the balanced state, when the M 2 muscles relax after a major contraction. When the M 1 and the M 2 muscles are contracted slightly, the balance of the system will be maintained, and when the M 1 and M 2 muscles are both strongly contracted, the whole proboscis will be slightly retracted.

The divergence of the M 2 muscles suggests that they are capable of producing slight lateral movements of the base of the proboscis—and hence of its distal end—when one or other of them contracts alone.

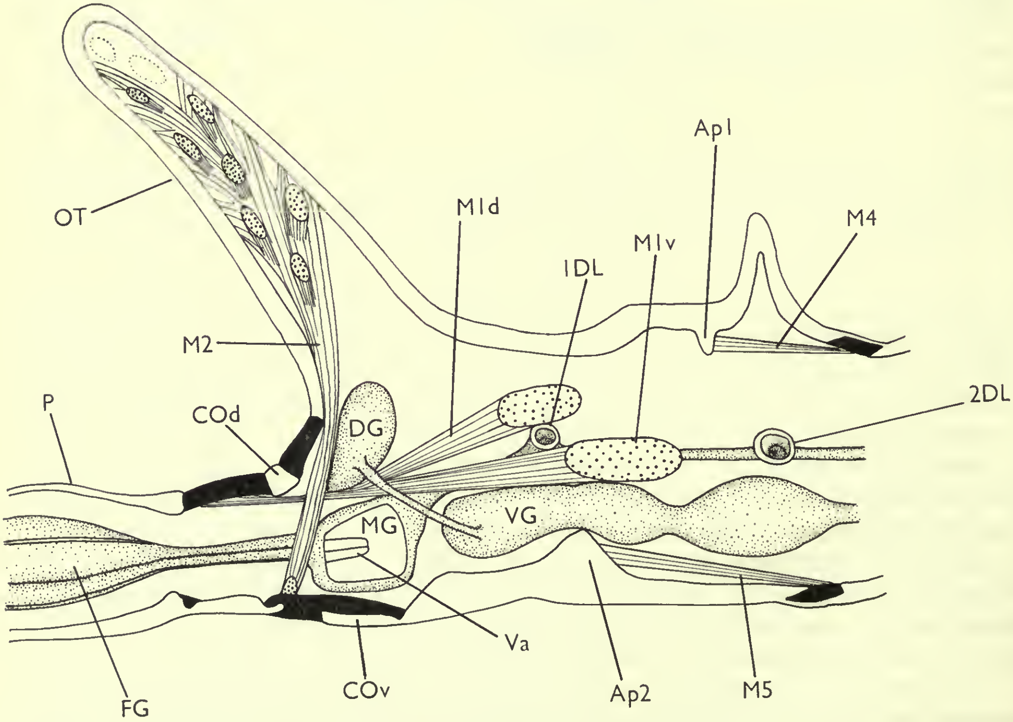

FIG. 4. Cephalic somite and proximal portion of the proboscis of *A. glaciale* seen in diagrammatic longitudinal optical section. Unsclerotized arthrodial membrane is shown as solid black. Only the structures of the left side are shown, except where portion of the midgut wall has been cut away to reveal the valve (Va) between fore- and midguts. See p. 223 for the key to the lettering.

In *Austrodecus glaciale* (Text-fig. 4) only two pairs of muscles are involved in moving the proboscis, but the region of articulation between proboscis and cephalic somite is more complicated than in either *Rh. australis* or *Pycnogonum stearnsi*.

The arthrodial region between proboscis and cephalic somite consists of two areas of unsclerotised membrane, separated by a collar of highly sclerotized cuticle (Text-fig. 4, Pl. 1. CO d and CO v). The proximal area of membrane is not continuous over the whole circumference of the joint, for the wide, ventral, portion of the sclerotized collar is continuous, through a thin layer of highly sclerotized cuticle, with the thick, red-staining, wall of the cephalic somite. The distal area of membrane is continuous over the whole circumference of the joint, forming a ring.

The M 1 muscles each have two areas of origin (M1 d and M1 v) on the lateral walls of the cephalic somite. The two portions of each muscle pass forward and merge almost immediately beneath the dorsal ganglion. The muscles then pass through the circumoesophageal commissure, through the sclerotized collar in the articulation, and insert on the arthrodial membrane immediately behind the dorsal proximal edge of the proboscis. During their passage forward the muscles converge.

The M 2 muscles are much more massive than the M 1 muscles. They have their origins over all the wall of the ocular tubercle, which is enormously elongated in this species. They pass almost straight downwards, outside the circumoesophageal commissure, and insert on the ventrolateral walls of the arthrodial membrane, immediately posterior to the proximal edge of the proboscis.

If anything, the difference in height between the origins and insertions of the M 1 muscles, and the angles that they made with the longitudinal axis of the trunk and proboscis, are less than in *Rh. australis*. But contraction of the M 1 muscles will produce strong tension forces in the anterior dorsal portion of the arthrodial membrane. Part of the force will be spent in causing that portion of the membrane to buckle inwards and slightly down, and part in making the sclerotized collar tilt about its posterior basal union with the floor of the cephalic somite. This will not only pull backwards the dorsal proximal edge of the proboscis, cause the whole proboscis to tilt about an axis in the plane of flexure of the arthrodial membrane, and thereby raise the tip of the proboscis, but will also cause slight raising of the whole proboscis.

The positions and shapes of the regions of arthrodial membrane and the collar provide two ventral hinges, about which the proboscis may tilt. The posterior hinge (the thin, sclerotized, cuticle joining the collar and cephalic somite) will allow the collar to tilt backwards only under the forces exerted by the M 1 muscles ; being very highly sclerotized, it will be highly elastic, and therefore considerable force will have to be generated around the hinge if the proboscis is to tilt about an axis in the plane of the hinge. The M 1 muscles are disposed so that their contraction will cause movement about the elastic hinge region with relatively little expenditure of energy. All but the most violent contractions of the M 2 muscles, on the other hand, will cause no movement about this elastic hinge region. The almost vertical direction of pull of the M 2 muscles will cause movement about the second hinge region—the anterior ventral portion of the arthrodial membrane.

Resolution of the forces exerted by the M 2 muscles in the joint between proboscis and cephalic somite shows that the major part of the forces will tend to raise the ventral proximal end of the proboscis, while only a very small component will tend to rotate the collar. It appears that the elasticity of the posterior ventral hinge region will safely counteract this small component, with the result that the proximal ventral edge of the proboscis will be tucked up inside the anterior ring of arthrodial membrane. Such a movement will cause the tip of the proboscis to be thrust downwards.

The size of the M 2 muscles in this species suggests that the tip of the proboscis can be moved ventrally with considerable force. Such a supposition agrees well with the suggested method of feeding described below (see p. 217).

The disposition of the muscles in this species does not suggest that the whole proboscis can be retracted, and in fact retraction of a strongly downcurved proboscis does not appear to be a very useful movement.

Pycnogonum stearnsi (Text-fig. 5) is similar to *A. glaciale* in that only two pairs of muscles are involved in moving the proboscis, and is similar to *Rh. australis* in possessing no sclerotized collar in the region of articulation, but is quite unlike either species in that the M 1 muscles do not pass through the circumoesophageal commissure.

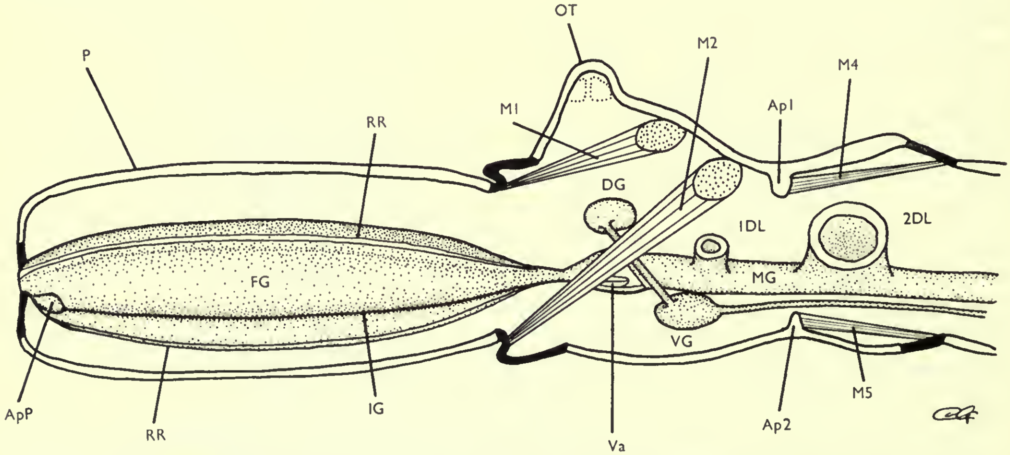

FIG. 5. Diagrammatic longitudinal optical section of the cephalic somite and proboscis of *P. stearnsi*. Unsclerotized arthrodial membrane is shown as solid black. Only structures of the left side are shown, except where a portion of the midgut wall has been removed to show the valve (Va) between midgut and foregut. See p. 223 for the key to the lettering.

The M 1 muscles have their origins on the dorsal wall of the cephalic somite, partly inside the ocular tubercle. They pass downwards and forwards immediately dorsal to the dorsal ganglion, and insert on the distal dorsal edge of the arthrodial membrane between proboscis and cephalic somite.

The M 2 muscles have their origins on the lateral walls of the cephalic somite, posterior to the regions of origin of the M 1 muscles. They pass forward and downward, outside the circumoesophageal commissure and insert on the ventrolateral walls of the arthrodial membrane.

As in the other species, the raising and lowering of the tip of the proboscis appears to be brought about by contraction of the M 1 and M 2 muscles respectively. As in *Rh. australis,* the relatively small angles which the muscles make with the longitudinal axis of the body suggest that the vertical movements of the proboscis are unlikely to be very powerful.

Contraction of both M 1 and M 2 muscles together will tend to retract the whole proboscis, and it seems reasonable to suppose that the proboscis is retracted during feeding movements. Unlike the situation in *A. glaciale,* where the proboscis is strongly downcurved, it appears that retraction of a straight proboscis, from massive, soft, food material, is a useful movement.

Taxonomic significance of the disposition of the extrinsic muscles.

While the internal structures of the proboscis have been the subject of several studies, the nature and disposition of the extrinsic proboscis musculature has received very little attention.

Dohrn (1881) was the first to illustrate the musculature, but his figures suggest that he could not interpret with any certainty the structures that he observed. This is doubtless due to the fact that he examined his specimens as solid, transparent, objects, and neither sectioned nor dissected them. Hoek (1881) appears to be the only other author to describe or illustrate the extrinsic musculature of the proboscis,* and while his figure of the transverse sectional appearance of the cephalic somite of *Colossendeis leptorhynchus* Hoek (Pl. 18, fig. 7) is in some respects more informative of the disposition of proboscis muscles than the figures by Dohrn, it gives no indication of the sites of origin and insertion of muscles. Neither of these authors discusses the extrinsic proboscis musculature other than by way of a passing reference in the text.

Dohrn (loc. cit.) illustrated part or all of the extrinsic musculature of *Ascorhynchus* (= *Barana*) *castelli* Dohrn, *Achelia echinata* Hodge (= *Ammothea fibulifera* Dohrn), and *Achelia* (= *Ammothea*) *langi* Dohrn. According to the figures in all three species the muscles retracting the upper surface of the proboscis (= M 1 muscles) originate on the dorsal wall of the cephalic somite, behind the ocular tubercle. In *A. castelli* and *Ach. echinata* the M 1 muscles consist of a single pair, which passes forward through the circumoesophageal commissure to its insertions on the dorsal edge of the proboscis. In *Ach. langi* (Dohrn, 1881, Pl. 5, fig. 4), on the other hand, the M 1 muscles consist of two pairs, and while the member of each pair with the more ventral origin in the wall of the cephalic somite runs forward through the circumoesophageal commissure, the member of the pair of more dorsal origin runs over and in front of the dorsal ganglion. Thus, while in *Rh. australis* the members of each pair of M 1 muscles meet posterior and ventral to the dorsal ganglion, in *Achelia langi* they meet anterior and dorsal to the dorsal ganglion.

Dohrn's figures of *Ascorhynchus castelli* (1881, Pl. 1, fig. 2) indicates that the muscles retracting the base of the proboscis (= M 2 muscles) originate inside the anterior surface of the ocular tubercle, and under the cephalic lobes. This condition is very similar to that observed in *Austrodecus glaciale*.

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*Helfer & Schlottke (1935) simply reproduce Dohrn's figure of *A. castelli,* and do not comment on it.

It is apparent that the proboscis of most, if not all, the species of *Ascorhynchus* is highly mobile in a vertical plane, and can be moved so as to lie almost parallel with the trunk. It is not surprising, therefore, to find that the M 2 muscles follow the same course as they do in *A. glaciale*, although in the latter species the muscles appear to produce small movements of great power, instead of larger movements.

Dohrn's figure of *Achelia fibulifera* gives no indication of the disposition of the M 2 muscles in this species, but his illustration of *Ach. langi* suggests that here the M 2 muscles originate on the dorso-lateral surface of the cephalic somite.

Hoek's illustration of the cephalic somite of *Colossendeis leptorhynchus* (1881, Pl. 18, fig. 7) shows clearly the passage of the M 1 muscles through the circum-oesophageal commissure, while the level in the cephalic somite at which the section was made indicates that the M 2 muscles also have their origins on the dorsal wall of the cephalic somite, posterior to the ocular tubercle.

From amongst all the Pycnogonida there is information on the nature of the extrinsic proboscis musculature of only six species. These six species are drawn from five genera which have long been considered very distinct, on the grounds of their external morphology. It is, therefore, no surprise to find that, in general, the dispositions of the extrinsic proboscis muscles differ widely amongst the five genera. Two points are worthy of remark. The first is the striking dissimilarity between two species of the same, long established, genus, (*Achelia echinata* and *Ach. langi*), and the second is the similarity between *Rhynchothorax australis*, *Achelia echinata*, and *Colossendeis leptorhynchus*, which are members of three long separated genera.

Previous interpretations of the Morphology of the Proboscis.

Longitudinal, transverse, and horizontal sections of the three species reveal that not one of the previous interpretations of the structure and functioning of the proboscis is entirely adequate.

The structure of the proboscis was first elucidated by Dohrn (1881) for *Trygaeus communis* Dohrn, and for *Phoxichilus vulgaris* Dohrn and *Ph. charybdaeus* Dohrn (both = *Endeis spinosa* Montagu). Hoek (1881) examined the structures in the proboscis of *Nymphon robustum* Bell and Wirén (1918), in his discussion of the morphology and phylogeny of the Pycnogonida, gave a highly detailed description of the nervous system of the proboscis of *Nymphon brevirostre* Hodge.

The only other author to discuss in detail the structures within the pycnogonid proboscis has been Henry (1953), who did not concern herself with musculature.

The structures which Dohrn and Hoek claim to have found in the species that they studied are shown in Text-fig. 6.

The Alimentary Canal.

The cavity of the alimentary canal within the proboscis is lined with cuticle, which is continuous anteriorly with the outer cuticle of the proboscis. No tissues have ever been described as occurring inside this cuticular wall, although it is lost and renewed at ecdysis.

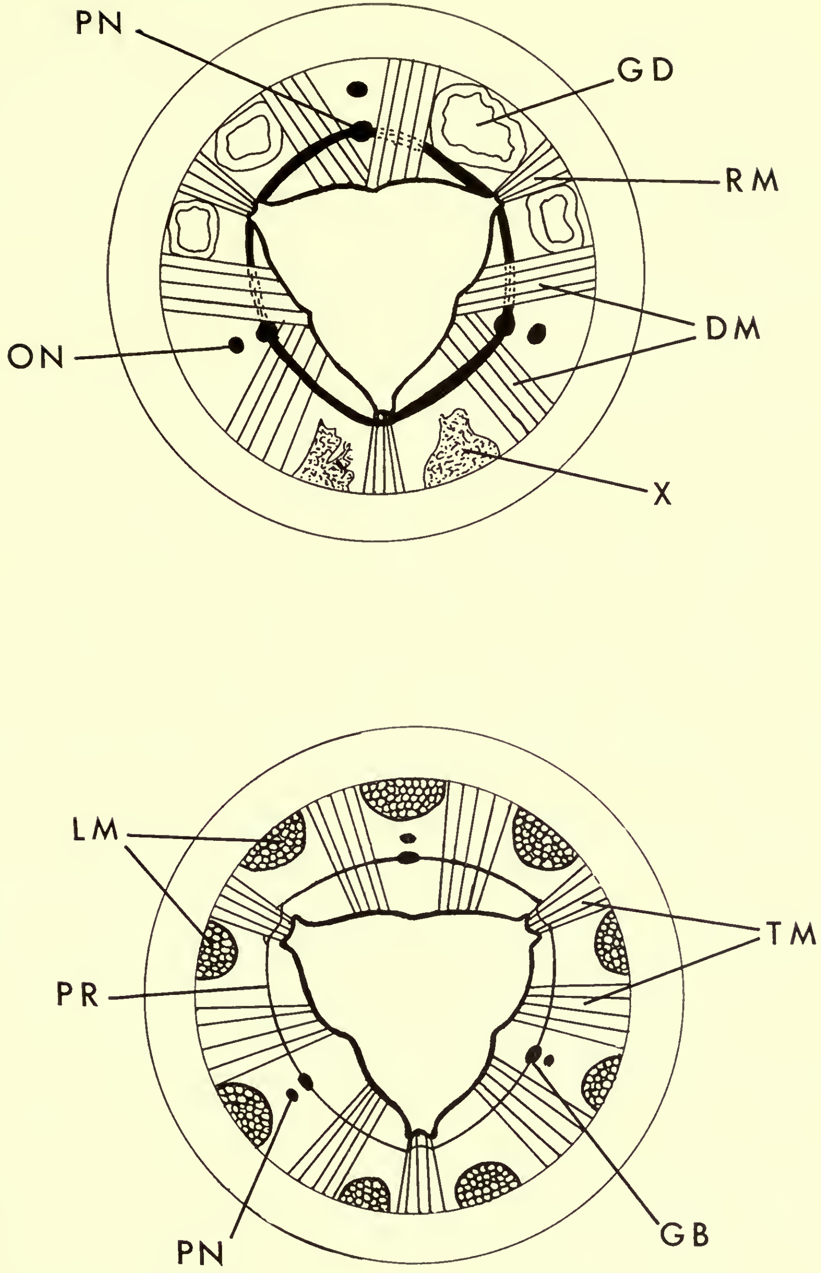

Fig. 6. Two early interpretations of the structures of the pycnogonid proboscis, as shown in transverse section. *Above:* interpretation by Dohrn (1881) of the proboscides of *Trygaeus communis* Dohrn and *Endeis spinosa* Phillippi. *Below:* interpretation by Hoek (1881) of the proboscis of *Nymphon robustum* Bell. See p. 223 for the key to the lettering.

The cross-sectional shape of this foregut lumen reflects the basic triradial symmetry of the proboscis (see above, p. 204), which arises from the fusion of a single dorsal and two ventrolateral antimeres. Thus, throughout its length the foregut is trifoliate in cross-section, although in regions of greatest cross-sectional area the shape may approach that of an equilateral triangle. For the purposes of this discussion, the ridges of the foregut (Text-fig. 7 R), which mark the boundaries between the three antimeres, are referred to as radial, while the walls between the ridges are considered to be interradial.

Throughout all the length of the foregut in the three species studied, the radial ridges are thicker than the interradial walls, but each interradial wall bears a groove (Text-fig. 7, IRG) whose floor is thickened.

In the proximal third of its length in the species so far studied, the foregut wall bears annular bands of red-staining thickened cuticle (Pl. 2, AT). These bands bear fine, long, setae which project forwards and slightly inwards, so that the entire lumen of the foregut in this region is filled with a fine meshwork (Text-fig. 7, Pl. 2, 4, 5. FS.). It appears that this structure acts both as a mechanism for macerating tissues ingested by the pycnogonids, and also as a filter, which prevents the passage of large, hard, objects into the narrow posterior end of the foregut.

While the cross-sectional area of the anterior portions of the foregut may vary differently in different species, in all the species studied so far the cross-sectional area of the foregut decreases abruptly in the proximal third of its length.

In all three species the foregut empties into the midgut through a very narrow tube which is carried well into the lumen of the midgut in a papilla (Text-figs. 4 and 5, Pl. 2 Va). It would appear that this papilla must act as a very simple non-return valve (see p. 216).

The outer wall of the proboscis and the lips.

In *P. stearnsi* and *Rh. australis* the wall of the proboscis is composed of uniformly red-staining, thick cuticle, except where the outer wall merges into the walls of the lips. In *A. glaciale* the proboscis wall is quite different in appearance. Where the proboscis is narrow and downcurved, the wall consists of a thick, non-staining, matrix of cuticle, which bears fine annular grooves set closely together at regular intervals. At the base of each groove and extending to the inner surface of the proboscis wall is a ring of cuticle which stains dark red. The muscles which produce changes in the foregut volume are all inserted into the red-staining rings. In the more proximal regions of the proboscis, the wall is uniformly red-staining and is similar in appearance to the proboscis walls of *P. stearnsi* and *Rh. australis*.

If it is accepted that the non-staining, highly refractile, cuticle is more elastic than the red-staining cuticle, then it appears that the narrow portion of the proboscis of *A. glaciale* is flexible, and that the flexibility has been achieved without any loss of efficiency of the muscles which alter the foregut volume, since these muscles are attached to highly inelastic cuticle. Conversely, the proboscides of *P. stearnsi* and *Rh. australis* are unlikely to undergo any alterations in shape.

The three lip lobes of the proboscis are more strongly developed in *P. stearnsi* and *Rh. australis* than in *A. glaciale*. In *P. stearnsi* all three lips are of approximately equal size, whereas in *Rh. australis* the dorsal lip is much smaller than the two ventrolateral lips.

In *Rh. australis* and *P. stearnsi* the interradial portions of the end of the proboscis are composed of arthrodial membrane, while the radial ridges of the foregut are firmly anchored to the outer proboscis wall by non-staining, refractile, cuticle. At the mouth aperture itself, and for a short distance posterior to the aperture, the interradial grooves of the foregut are enormously thickened with non-staining, refractile cuticle, which is expanded backwards and outwards, into large apophyses (Text-figs. 3, 5 and 7, Pl. 3 fig. 1, ApP). To these apophyses are attached the tendons of the lip muscles (Text-fig. 7, Lpt, LpM). In *P. stearnsi* a lip apophysis occurs on each interradial groove, while in *Rh. australis* the interradial groove of the dorsal antimere is devoid of an apophysis. Of all the structures observed in the proboscides of the three species, the lip apophysis and musculature alone depart from the basic triradial symmetry.

The Intrinsic Musculature of the Proboscis.

In the three species which were the object of this study, four functionally distinct types of muscles can be seen. The muscles of all four types—and indeed all the muscles which have been observed in the Pycnogonida—are striated (Pl. 4).

The radial muscles (Text-fig. 7, Pl. 3, 4 and 5, RaM) occur throughout the entire lengths of the proboscides of the three species. They connect the thickened radial ridges of the foregut to the inner surface of the proboscis wall.

In any one plane, a pair of interradial muscles can be seen in each of the three interradii of the proboscis. These muscles are inserted immediately on either side of the thickened interradial grooves of the foregut wall, and they pass outwards to the inner surface of the proboscis wall (Text-fig. 7, Pl. 3 and 4, IRM). Dohrn (Text-fig. 6, DM) depicted the interradial muscles as overlapping in their regions of insertion on the foregut wall. This condition cannot be observed in the three species described here.

In *A. glaciale* and *Rh. australis* the radial and interradial muscles occur as numerous rings of muscles, all the components of each ring lying in the same plane, at right angles to the longitudinal axis of the proboscis. In *P. stearnsi* the interradial muscles are arranged as in the other two species, but in the proximal two thirds of the proboscis the radial muscles run oblique to the long axis of the proboscis, so that their insertions on the foregut wall lie slightly posterior to their origins on the surface of the proboscis wall.

The third type of muscle is the circular muscle (Text-fig. 7, Pl. 4, 5 CM) which occurs only in the proximal region of the foregut, where the foregut cross-sectional area decreases abruptly. Each circle of muscles consists of three arcs of fibres, which are inserted at both ends on to the thickened radial ridges of the foregut. The rings of circular muscles alternate with the rings of radial and interradial muscle fibres.

Dohrn, Hoek, Wirén (loc. cit.) all interpreted these circular muscles as nerve fibres (Text-fig. 6, PR) linking three longitudinal nerve fibres, and innervating the radial and interradial muscles. The clearly striated nature of the circular fibres, and their insertions on the radial ridges of the foregut leave no doubt that the fibres are contractile, and not nervous, in function.

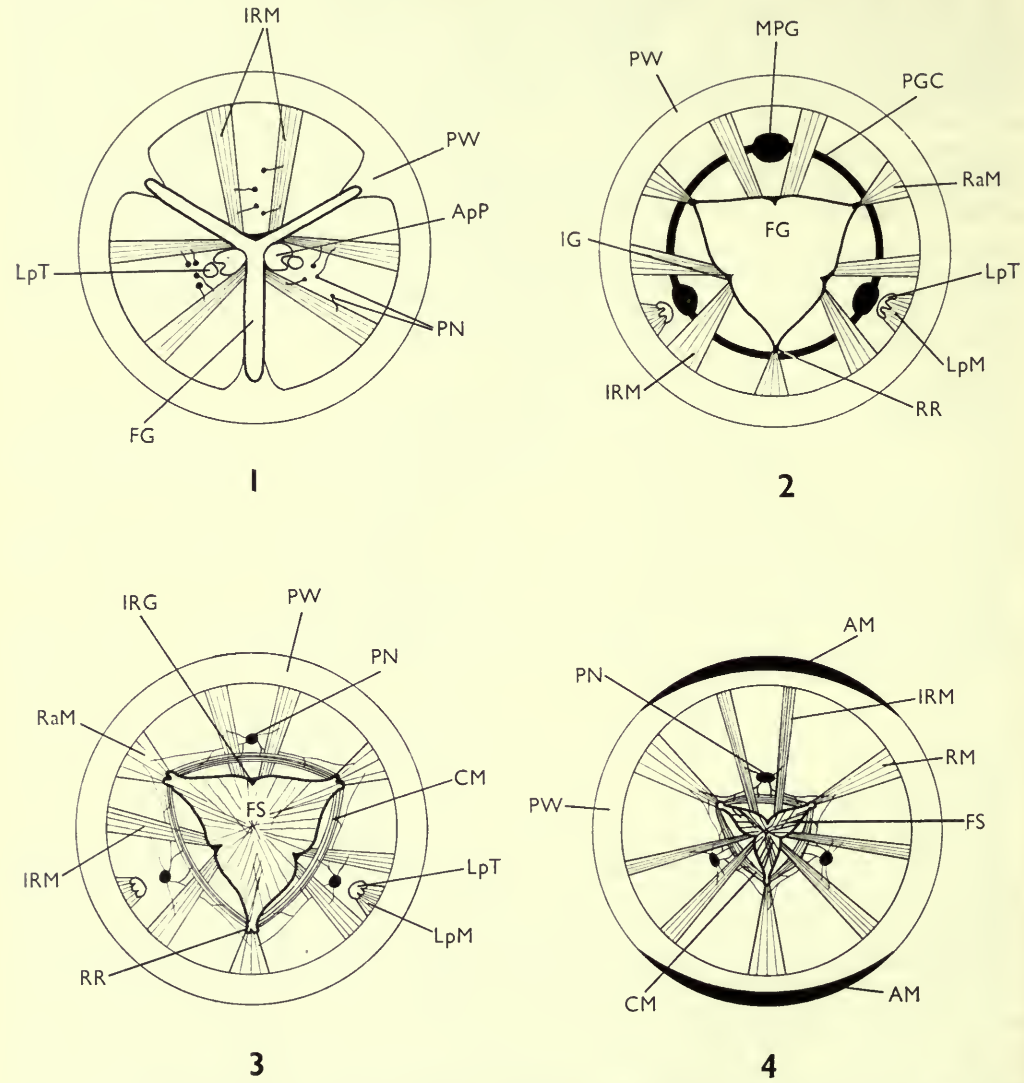
IRM
PW
ApP
LpT
PN
FG
1
MPG
PW
PGC
RaM
FG
IG
LpT
LpM
IRM
RR
2
IRG
PW
PN
RaM
CM
FS
IRM
LpT
LpM
RR
3
AM
PN
IRM
RM
PW
FS
CM
AM
4

Fig. 7. Interpretation of the structures of the proboscides of *Rh. australis*, *A. glaciale* and *P. stearnsi*, as shown by transverse sections. 1. Section immediately posterior to the anterior surface of the proboscis of *Rh. australis* ; 2. Section at the level of the main proboscis ganglia, in *Rh. australis* ; 3. Section posterior to section 2, in *Rh. australis* ; 4. Section at the level of the insertion of the proboscis into the cephalic somite, in all three species. Sections 1, 2, and 3, differ from the sections at the same levels in *A. glaciale* only in the presence of lip musculature, tendons and apophysis, and from sections of *P. stearnsi* only in the absence of the dorsal lip musculature. See p. 223 for the key to the lettering.

The three longitudinal nerve fibres do exist and in most sections they lie very close to the circular muscles. However, under phase contrast illumination, fine nerves can be traced from the longitudinal nerve trunks to the radial, the interradial, and the circular muscles.

The fourth type of musculature—the lip muscles—occurs only in *P. stearnsi* and *Rh. australis* (Text-fig. 7, Pl. 3, 5 fig. 1, LpM). In both species, the muscles originate on the inner surface of the proboscis wall, and run obliquely forwards to their insertions on a tendon (Text-fig. 7, LpT) which is attached to the large lip apophyses of the two ventrolateral antimeres. In *P. stearnsi* only a third lip muscle with its tendon and lip apophysis lies in the dorsal antimere. The muscles and their tendons lie between the interradial muscles of each antimere.

Dohrn (loc. cit.) gives no indication of finding similar lip musculature in the species that he studied, but describes three sets of muscles which are apparently modified anterior interradial muscles. These muscles ("Retraktoren der Lippen") are little longer than the normal interradial muscles. Wirén (loc. cit.) describes a similar but slightly more complicated modification of three sets of interradial muscles in *Nymphon mixtum* Kröyer.

Hoek (loc. cit.), on the other hand, describes no less than nine bundles of longitudinal muscles (Text-fig. 6, LM) in *N. robustum*, but does not indicate their sites of insertion, nor did he hazard any guesses as to their functions. Doubtless, some of the structures that he considered to be longitudinal muscles are the diverticula of the gut and the gonad which appear to extend almost to the tip of the proboscis in all pycnogonids, (Pl. 4, GND).

The Nervous system of the Proboscis.

All of the previously published descriptions of the nervous system of the proboscis have agreed on the general pattern of innervation of the muscles. Sections of *P. stearnsi*, *Rh. australis* and *A. glaciale* suggest either that the previously described species differ markedly from these three, or else that earlier authors have been misled by the original interpretation of the circular muscles as rings of nerves.

Wirén (loc. cit.) has given the most comprehensive account of the nervous system of a pycnogonid, and all subsequent descriptions have differed but little from the basic plan envisaged by him. Essentially, Wirén's description indicates three major proboscis nerves, one for each antimere. The dorsal antimere receives its major nerve from the dorsal ganglion of the brain, and each of the ventrolateral antimeres receives its major nerve from one side of the ventral ganglion of the brain. These three nerves run forward to three large proboscis ganglia, situated just behind the tip of the proboscis, which are linked by circular fibres. Nerves run forward from the proboscis ganglia to a group of three small ganglia in each antimere. Wirén considered that these small ganglia, which are all interconnected, control the movement of the lips. From the three main proboscis ganglia there run backwards, inside the main proboscis nerves, three nerve trunks which are linked, at regular intervals, by circular nerve fibres. Small nerves from these circular fibres run to the radial and interradial muscles. Wirén depicts the circular nerve fibres in the proximal portion of the proboscis only, and as he described no other circular strands in the proboscis, and as the radial and interradial muscles occur throughout the whole length of the proboscis, it seems highly likely that his " circular nerve fibres " are, in fact, the circular muscle fibres which are so clearly distinguishable in the three species discussed here.

In all three species there are three main nerve trunks, with origins and positions similar to those depicted by Wirén. These three main nerves terminate in ganglia situated well behind the tip of the proboscis ; the ganglia are joined by arcs of stout nerve fibres. There are, however, no smaller lip ganglia anterior to the main ganglia. This is not surprising, since in *A. glaciale* there are no special lip muscles, while in *P. stearnsi* and *Rh. australis* the major part of the lip musculature lies posterior to the main ganglia. In the latter two species, a group of fine nerves runs back from the main ganglia above the main proboscis nerves, and gives off branches to the lip muscles.

Posterior to the main proboscis ganglia each main proboscis nerve consists of a group of fine fibres, rather than a single nerve trunk, although in places these fibres form a bundle. From the fibres, very fine nerves can be traced, running to the radial, the interradial, and—in the most proximal region of the proboscis–the circular muscles.

Methods of functioning of the proboscis.

It appears that the elasticity of the foregut wall is the major antagonist of the radial and the interradial muscles.

Contraction of the interradial muscles will cause the interradial walls of the foregut to be pulled towards the wall of the proboscis. The force applied by the interradial muscles will produce tension forces in the thickened floor of each interradial groove, and also tension forces in the thickened radial ridges. Contraction of the radial muscles, at the same time as the interradial muscles, will produce additional tension forces in both the interradial grooves and radial ridges. The radial muscles act, at the same time, as struts by which the whole foregut is kept in constant position within the proboscis lumen.

The overall result of the contraction of these two sets of muscles will be to change the cross-sectional shape of the foregut from trifoliate to more nearly triangular. As the foregut cross-sectional shape changes, so the volume of the foregut will increase. The lowering of pressure of the foregut lumen will produce an inrush of material from outside the animal, when the lips are open.

Relaxation of the radial and interradial muscles will release the tension forces engendered in the foregut grooves and ridges. These forces will tend to return the foregut to its original, trifoliate, cross-sectional shape. The volume of the trifoliate section foregut is less than when the foregut is triangular in section, and therefore the pressure of the foregut contents will rise when the tension forces in the foregut walls are released. If the lips are securely closed, and the rings of radial and interradial muscles relaxed, the foregut contents will be forced backwards.

However, the foregut cross-sectional area decreases markedly along the proximal third of its length, and strong frictional resistance will be engendered by the backward passage of material through this region. Resistance to movement of gut contents will be further increased in the proximal regions of the proboscis by the dense filter of setae projecting into the lumen.

However, it is along the proximal third of the length of the foregut that the circular muscles occur. The antagonist of these muscles is the chitinous foregut wall, which is here greatly reinforced by thick annular bands, bearing the setae which form the dense filter. Alternate contraction and relaxation of the radial and interradial muscles in this region will produce variations in the cross-sectional area of the foregut. Reduction of cross-sectional area of the foregut, following relaxation of the radial and interradial muscles, will be further assisted by contraction of the circular muscles.

The movements of the foregut wall will cause movements of the setae forming the filter. When the foregut contents anterior to the filter are under pressure, this movement of the setae will result in the food material being gradually pushed backwards through the filter and eventually into the midgut, being finely macerated as it moves through the filter.

It does not appear possible for the haemocoelic and other fluid spaces in the pycnogonids to act as the antagonists of the radial and interradial muscles and the mechanism described above would work equally well if the body fluids were not of fixed volume. It does appear likely, however, that hydrostatic pressure of the body fluids does play a part in ensuring the closure of the mouth.

When the volume of the foregut increases, the hydrostatic pressure of all the body fluids will be increased, as there is no separation of proboscis and trunk haemocoelic spaces. This rise of pressure will tend to force the proboscis forward, further into the material which it is ingesting. The hydrostatic pressure of the body spaces will remain high, even when food is being pushed backwards into the midgut. Thus when the lip musculature is relaxed, and the food is being forced back into the midgut, the tip of the proboscis will remain pushed into the food material. The only process which will lower the animals' internal pressure after food has been ingested is the evacuation of faeces from the hindgut.

The opening and closing of the lips is readily understood if the degree and distribution of sclerotization of the end of the proboscis is borne in mind. The interradial lip apophyses (ApP) are connected with the highly sclerotized proboscis wall by a region of arthrodial membrane. When tension is applied to the lip tendons, by contraction of the lip muscles, the interradial walls of the foregut will be pulled backwards and upwards, and the mouth opened. Closure of the mouth is achieved by the release of tension forces engendered in the enormously thickened interradial grooves of the lips during the opening of the mouth.

MORPHOLOGICAL ADAPTATIONS TO PREFERRED FOOD MATERIALS

The clear preference shown by *A. glaciale* for a single species of polyzoan, *Cellarinella foveolata* (Waters) (Br 3), can be interpreted readily in terms of the functional anatomy of the pycnogonid and the polyzoan. *A. glaciale* is obviously highly adapted to feeding on this particular form of polyzoan.

Two sets of characters of the polyzoan zooecia and colonies appear to be critical in determining whether or not a particular species of polyzoan is available to *A.*

glaciale as food. These are (a) the presence or absence of frontal wall pores, and their diameters, and (b) the shape, size and strength of the polyzoan colonies.

It seems highly unlikely that *A. glaciale* is capable of piercing the frontal wall of a zooecium, even if a zooecium is not heavily chitinised or calcified. Penetration to the polypide through the operculum is fraught with danger. Even if the pycnogonid were able to place its proboscis in the orifice, the closing operculum, which is usually very thick, would probably crush it. Furthermore, the polyzoan orifice may be screened by an avicularium. The movable jaw of the avicularia in *Camptoplites bicornis* (Br 4) and *Notoplites drygalski* (Br 2) is as much as 0·08 mm. in diameter, and could doubtless inflict considerable damage on the pycnogonid proboscis should the proboscis lie within the jaws during one of their sporadic closures.

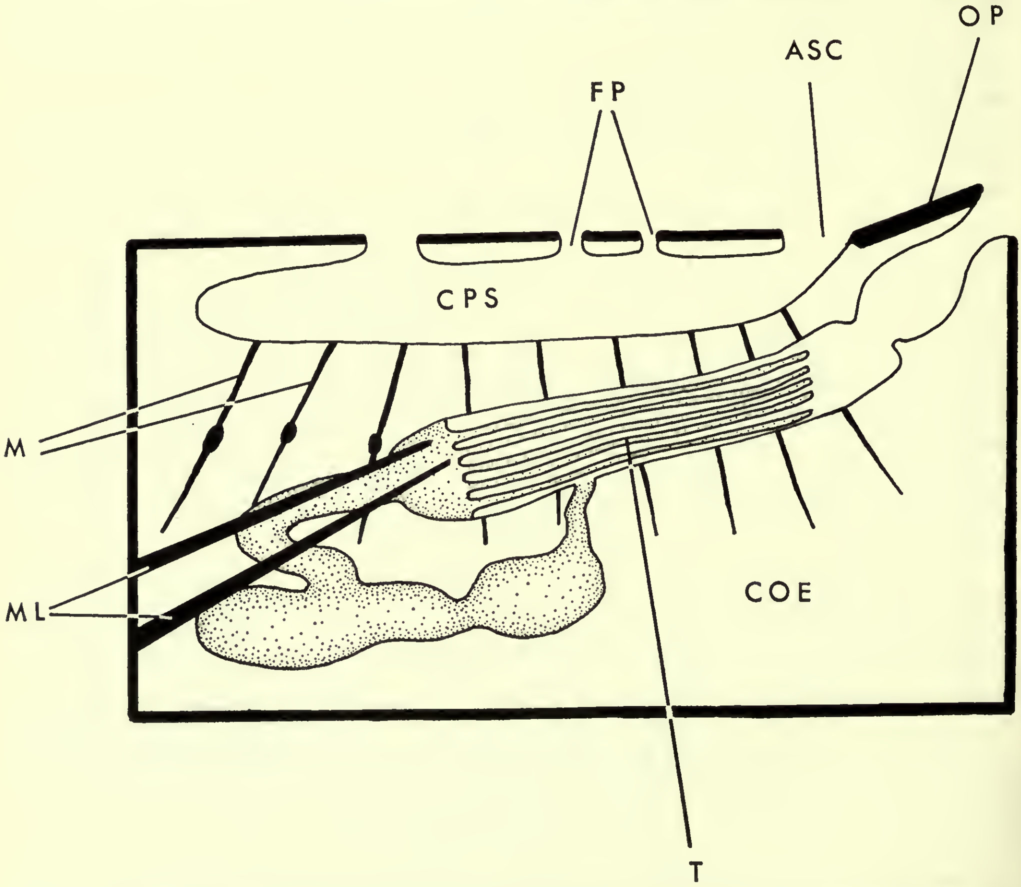

FIG. 8. Diagrammatic longitudinal optical section of the zooecium of *Cellarinella foveolata* (Waters) (Polyzoa Ectoprocta Ascophora), showing the structures which bring about the protrusion and retraction of the lophophore. See p. 223 for the key to the lettering.

It would appear that the fine distal portion of the proboscis is used to probe through the frontal wall pores of the zooecium, through the compensation sac, and into the coelom of the polypide. The frontal wall pores are rarely straight tubes, and the flexibility of the distal portion of the proboscis, which will allow it to traverse an irregular tube, is an obvious advantage to the pycnogonid. The disposition and size of the M 2 extrinsic muscles suggests that the tip of the proboscis can be pressed downwards with considerable force. Such force must be required to rupture the walls of the compensation sac and gain access to the coelom of the polypide.

A considerable advantage to the pycnogonid of piercing the compensation sac is that the tentacles of the polypide cannot be extruded once the compensation sac is ruptured (see Text-fig. 8). Presumably the polypide will retract as the pycnogonid investigates the frontal wall of the zooecium with its palps, and then begins to probe the frontal pores. Once the compensation sac has been punctured the pycnogonid can feed at leisure on the entire polypide.

The adults of *A. glaciale* have a leg span of approximately 10 mm. If a polyzoan colony has a width or circumference of very much less than 10 mm. the pycnogonid will be unable to anchor itself firmly while thrusting downwards with its proboscis. Alternatively, a widely spread colony of many fine branches with rigid nodes will provide as firm a platform upon which the animals can cling and feed as will a single firm, stout, branch.

TABLE IV

Br 1. *Cellarinella laytoni*
Shape : Cylindrical
Diameter : 0·8 to 2·0 mm.
Branches : Firm
Frontal Pores : Present, av. diam. 0·06 mm.

Br 2a. *Escharoides bubeccata*
Shape : Cylindrical
Diameter : av. 1·15 mm.
Branches : Firm
Frontal Pores : v. few, peripheral, partly concealed, av. diam. 0·04 mm.

Br 2b. *Notoplites drygalski*
Shape : Cylindrical
Diameter : av. 0·75 mm.
Branches : Flexible
Frontal Pores : Absent

Br 3. *Cellarinella foveolata*
Shape : Broad and Flat
Width : 2 to 40 mm.
Colony : Firm
Frontal Pores : Numerous, diam. 0·02 to 0·12 mm.

Br 4a. *Camptoplites bicornis*
Shape : Cylindrical
Diameter : av. 0·75 mm.
Branches : Flexible
Frontal Pores : Absent

Br 4b. *Cellarinella wandeli*
Shape : Cylindrical
Diameter : 0·6 to 0·9 mm.
Branches : Firm
Frontal Pores : Absent

Br 5a. *Cellaria vitrimuralis*
Shape : Cylindrical
Diameter : av. 0·75 mm.
Branches : Firm
Frontal Pores : Absent

Br 5b. *Cellaria moniliorata*
Shape : Cylindrical
Diameter : 0·3 to 0·5 mm.
Branches : Firm
Frontal Pores : Absent

The distribution of the two sets of characters amongst the eight species of Polyzoa concerned in the study is shown in Table IV. Amongst the eight species, only *Cellarinella foveolata* (Br 3) fulfills the conditions of a broad, firm, colony, whose frontal walls bear large numbers of pores of sufficiently large diameter to allow easy access for the proboscis of *A. glaciale* to the underlying polypide.

Pycnogonids have been reported as associating with specimens of virtually all of the phyla whose representatives occur in the sea (see Helfer & Schlottke 1935, pp.

198–201), and the main food source of at least twenty species of pycnogonids is known with some certainty. The food of these species is, variously, Hydrozoa, Scyphozoa, Actinozoa, nudibranchs, polychaetes, holothuria, and lamellibranch molluscs. While Dohrn (1881), Prell (1910), and Helfer (1909), have reported the spatial association of *Ascorhynchus arenicola* (Dohrn), *Phoxichilidium femoratum* Rathke, and *Anoplodactylus petiolatus* Krøyer with species of ectoproct Polyzoa, *A. glaciale* is the first species which can be said, with any confidence, to actually rely on Polyzoa for its main source of food.

It is unlikely that the universally slow-moving Pycnogonida would be capable of feeding solely on the retractable lophophores of polyzoans, and we would expect to find, in any other pycnogonids feeding mainly on Polyzoa, the same slim terminal portion of the proboscis as occurs in *A. glaciale*. With this in mind, it is reasonable to suppose that species of *Pantopipetta* Stock 1963 (= *Pipetta* Loman) are predators of Polyzoa. All the species of *Pantopipetta* occur in deep water, and their faunal associations—let alone their feeding behaviour—have never been described.

One species in the genus *Ammothea* Leach possesses the necessary modification of the proboscis for feeding on Polyzoa. This is *Ammothea stylirostris* Gordon. As the specific epithet implies, the proboscis is long in this species, and tapers to a small distal diameter. In the recently discovered juvenile of this species (Hedgpeth and Fry, in preparation) the proboscis is greatly elongated, and is drawn out to a minute terminal diameter. However, the palps are much shorter than the proboscis, and clearly in evolutionary process of atrophying. It is difficult to envisage the efficient use of a very long proboscis in probing small frontal pores, if the surface to be probed cannot be explored previously by the palps.

At least nineteen species of *Austrodecus* have been described, and in all but two the proboscis is long and styliform. In *A. frigorifugum* Stock the proboscis, while still of relatively small terminal diameter, is short, and bears a small distal bulb. In *A. breviceps* Gordon the proboscis is styliform, but is relatively very short. Amongst the other species there is some variation in the degree of curvature of the proboscis, and the ocular tubercle, which presumably provides the origins of the M 2 muscles throughout the genus, varies greatly in its height. It may well be that these variations of proboscis and ocular tubercle are closely correlated with the morphology of the various Polyzoa upon which the species feed.

The marked preference shown by *Rh. australis* for *Eudendrium tottoni* (Hy 1) amongst the Hydrozoa, is readily explicable. Of the four species of Hydroidea presented to the pycnogonids, *E. tottoni* alone is athecate. Whilst the hydrothecae of *Symplectoscyphus epizooticus* (Hy 2), *S. vanhoeffeni* (Hy 3), and *Hydrodendron arborea* (Hy 6) are sufficiently wide to allow the proboscis of *Rh. australis* easy access to contracted hydranths (see Totton 1930), the hydranths of *E. tottoni*, which cannot be withdrawn into a protective cup, will be discovered far more readily by accidental contact.

There is no obvious reason why the two species of Alcyonaria should occupy so low a position in the food preferences of *Rh. australis*, unless the nematocysts of *Thouarella variabilis* (Hy 4) and *Alcyonium paessleri* (Hy 5) are capable of penetrating the exoskeleton of the pycnogonid. Nematocysts do not deter various species of *Pycnogonum* from feeding on Actinia (Sars 1881, Mobius 1893, Prell 1910, Loman 1925, 1928, Stephenson 1933, Zeigler 1960, et al.). However, the Actinian organization, and the pattern of development of nematocysts, is such that by feeding at the base of the column the pycnogonids can avoid contact with functional nematocysts It is unlikely that *Rh. australis* could feed on either of the species of Alcyonaria without coming into contact with the hydranth nematocysts.

A far more likely explanation of a low preference for the alcyonarians is the fact that *Rh. australis* is not likely to encounter *Th. variabilis* or *A. paessleri* as frequently as it does the hydroids. In contrast to the hydroids, which grow in and on the surface of the substrate, the two alcyonarians are erect in form, and usually rise several centimetres above the surface of the substrate (see Bullivant 1959b, 1961). *Rh. australis* was always found either within the sponge spicule mat or at its surface

On the other hand, several large specimens of *Nymphon australe* Hodgson were taken on colonies of both species of Alcyonaria, and climbed on and clung to fragments of the alcyonarians kept in an aquarium in the laboratory.

As was stated above, there can be little doubt that the major food source of *P. stearnsi* is actinians, although small individuals are taken from amongst large hydroids. All told, approximately thirty species of Hydrozoa and Anthozoa are known to be either the food, the site of larval development, or at least the preferred substrate of fifteen species of pycnogonids. In all of these pycnogonid species the proboscis is bluntly rounded terminally and is of relatively large and uniform diameter throughout its length. Such a proboscis shape appears to be ideally suited for the ingestion of large pieces of soft coelenterate tissue. Since the tissues of the prey are relatively soft, the pycnogonids have no need for mechanisms for piercing or pushing hard against the prey. On the other hand the ingestion of large morsels of food requires that the mouth can be opened wide. It has been shown (above) that the lip opening musculature of *P. stearnsi* is more highly developed than that of *Rh. australis*.

The significance of the secondary bilateral symmetry of the lip musculature in *Rh. australis* is not readily apparent. Presumably this condition represents an adaption for preventing the mouth from opening widely, and it appears to be a very crude solution to such a need, unless the innervation of the lip musculature in Pycnogonida does not allow for partial opening or closing of the mouth [In other words, nervous stimulation of the lip muscles results only in all the muscle fibres being either fully contracted or fully relaxed]. It is an obvious advantage to the pycnogonid, which ingests food by suction, that the size of the mouth aperture should be closely related to the size of the food morsels to be ingested. *Rh. australis* and *P. stearnsi* must be able to generate enough suction to tear portions of hydrozoan tissue from their parent body. However great the suction power which can be generated, little tissue will be detached and ingested if sea water can enter the proboscis around the food material.

P. stearnsi inserts its proboscis deeply into a thick wall of anemone tissue, and therefore can ingest food through a very wide aperture. *Rh. australis*, on the other hand, must attach the tip of its proboscis, by suction, to a relatively very small hydroid polyp, which it must tear from the colony by suction. It can only do this efficiently if the mouth gape is always smaller than the polyps upon which it feeds.

This reduction of the mouth gape in *Rh. australis* does not appear to be an adaption for feeding solely on *E. tottoni* (Hy 1), but rather for feeding on any hydroids with small polyps, for all of the hydroids encountered in the environment have polyps of very similar dimensions (see Totton, loc. cit.).

The preferred foods of the two other species of *Rhynchothorax*—*Rh. mediterraneus* Costa and *Rh. philopsammum* Hedgpeth—are totally unknown. The proboscis of all three species are of similar size and shape, indicating ingestion of relatively large food particles.

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KEY TO LETTERING IN TEXT-FIGURES AND PLATES

AM	Arthrodial membrane
ApP	Interradial lip apophysis
Ap 1, 2	Apophyses
ASC	Ascopore of the compensation sac
AT	Annular sclerotization
CM	Circular muscles
COE	Coelom of polypide
CPS	Compensation sac
DG	Dorsal ganglion of the brain
1 DL	1st major midgut diverticulum
2 DL	2nd major midgut diverticulum
DM	Dilator muscles
FG	Foregut
FP	Frontal pores of compensation sac
FS	Filter of setae borne on annular sclerotizations
GB	Ganglionic bundle
GND	Gonad
IG	Interradial grooves of foregut
IRM	Interradial muscles
LM	Longitudinal muscle bundles
LpM	Lip muscles
LpT	Lip tendon
M	Muscles producing inflation of the compensation sac
MG	Midgut
ML	Muscles retracting the lophophore
MPG	Main proboscis ganglion
M1–3	Extrinsic proboscis muscles
M4, 5	Intersegmental muscles
ON	Outer nerve
OP	Operculum
OT	Ocular tubercle
P	Proboscis
PGC	Proboscideal ganglionic commissure
PN	Proboscis nerve
PW	Proboscis wall
RaM	Radial muscles
RM	Retractor muscles
RR	Radial ridges of the foregut
T	Retracted tentacles
TM	Transverse muscles
Va	Valve between foregut and midgut
VG	Ventral ganglion of brain
X	Tissues of unknown function

PLATE I

Longitudinal vertical section of the anterior portion of the trunk, and the base of the proboscis, of *A. glaciale*.

See p. 223 for the key to the lettering.

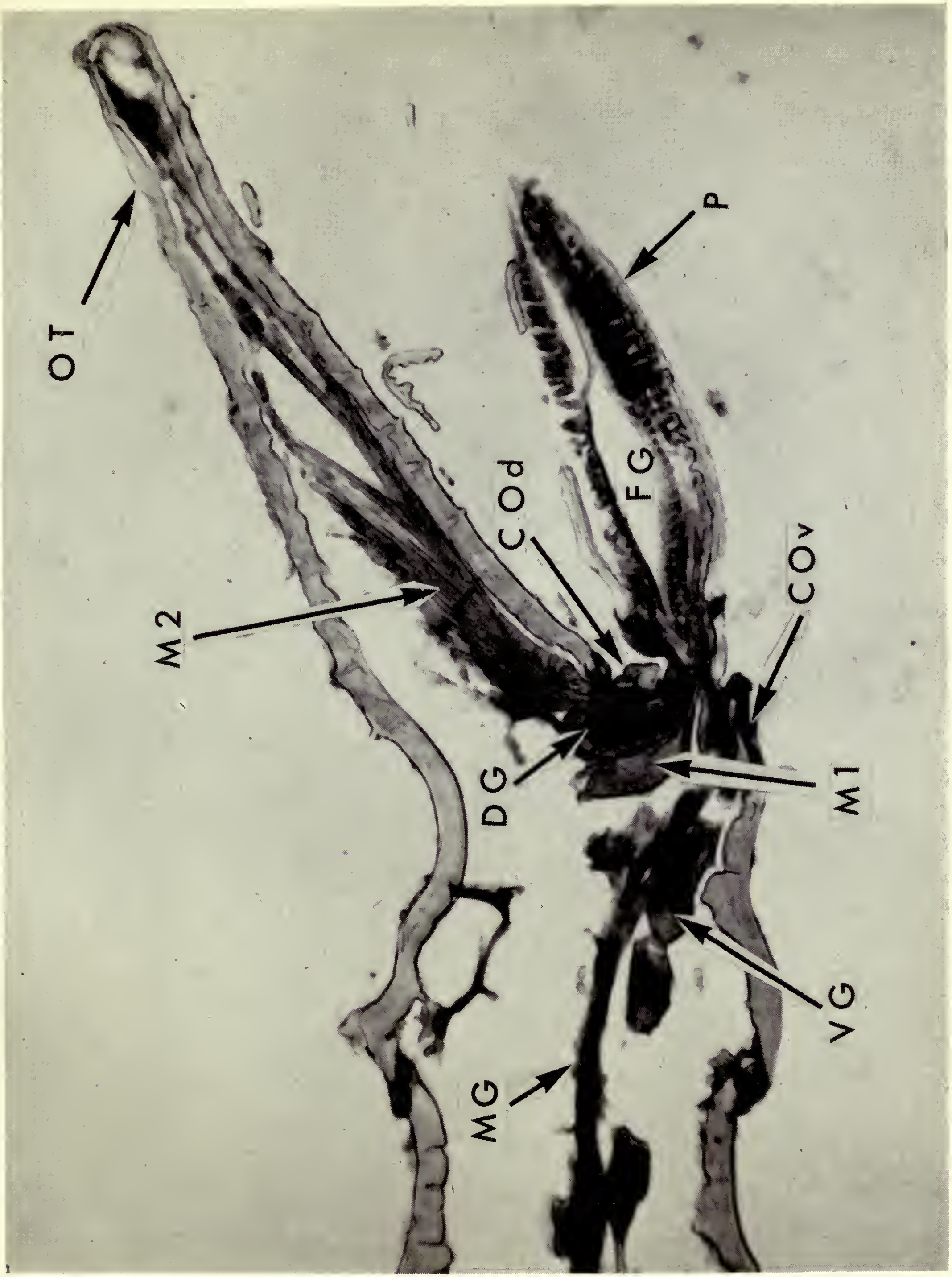

OT
P
FG
COd
M2
COv
DG
M1
VG
MG

PLATE 2

Longitudinal vertical section of the cephalic somite, and the base of the proboscis, of *P. stearnsi*.

See p. 223 for the key to the lettering.

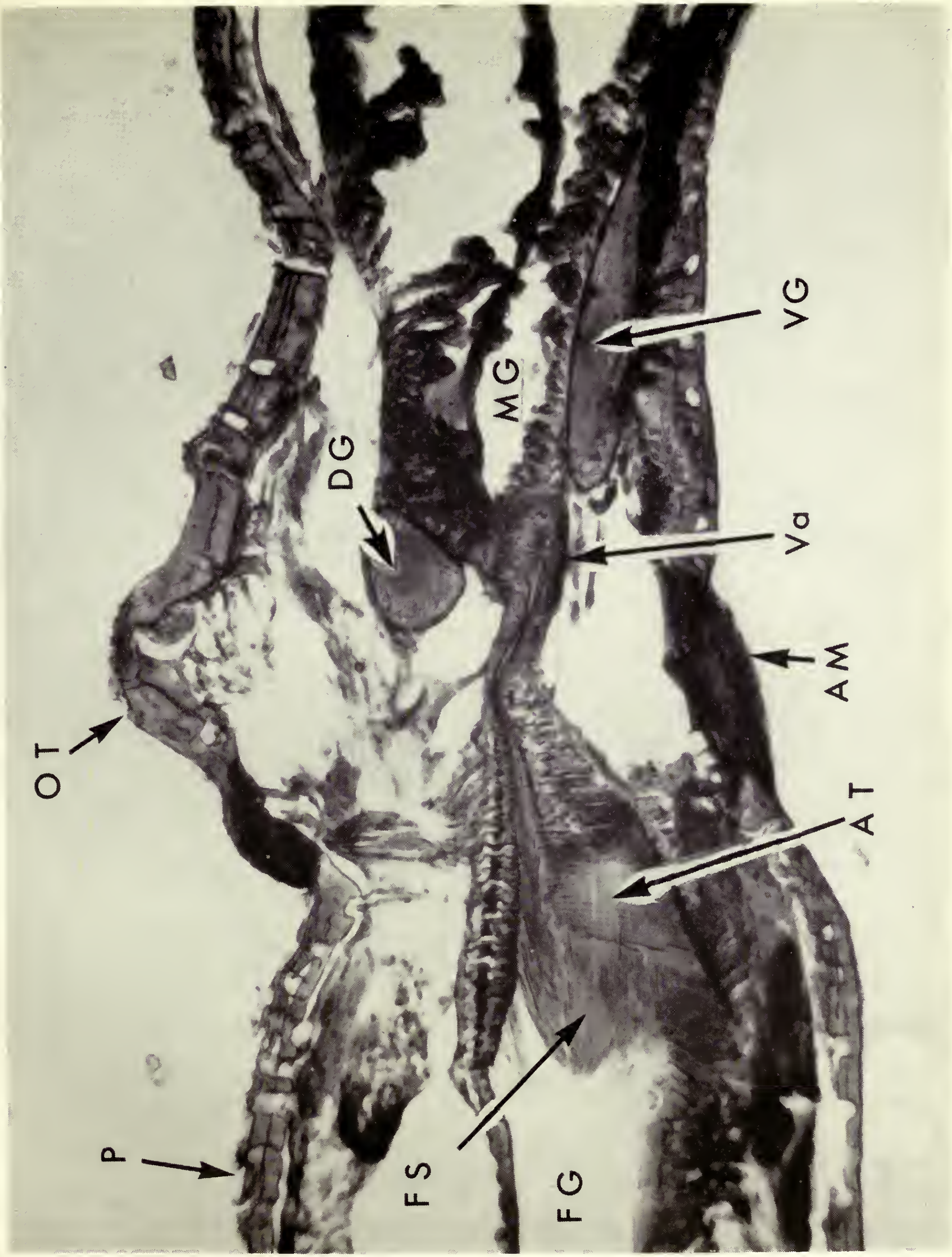
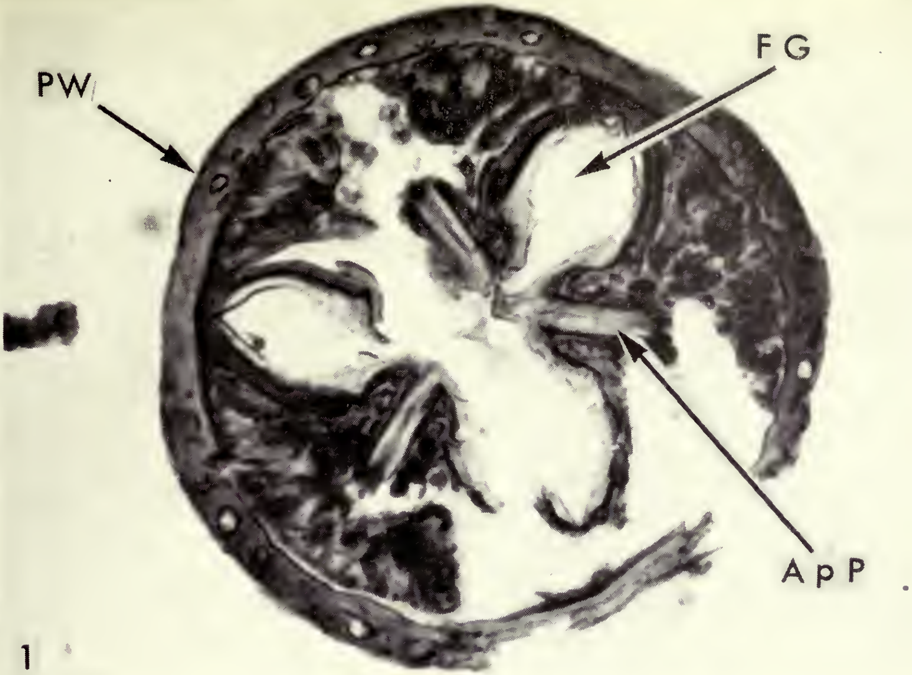

OT
P
DG
MG
VG
Va
AM
AT
FS
FG

PLATE 3

Transverse sections of the proboscis of *P. stearnsi*. (Upper) in a plane immediately posterior to the tip of the proboscis ; (Lower) posterior to (Upper) at the level of the main proboscis ganglia.

See p. 223 for the key to the lettering.


PW
FG
ApP
1

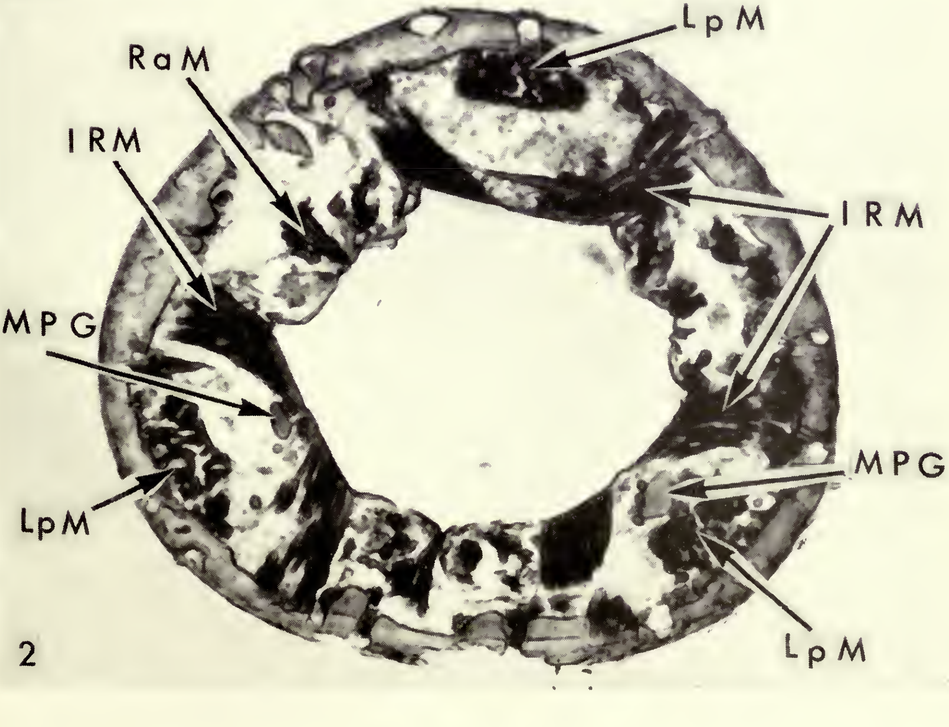
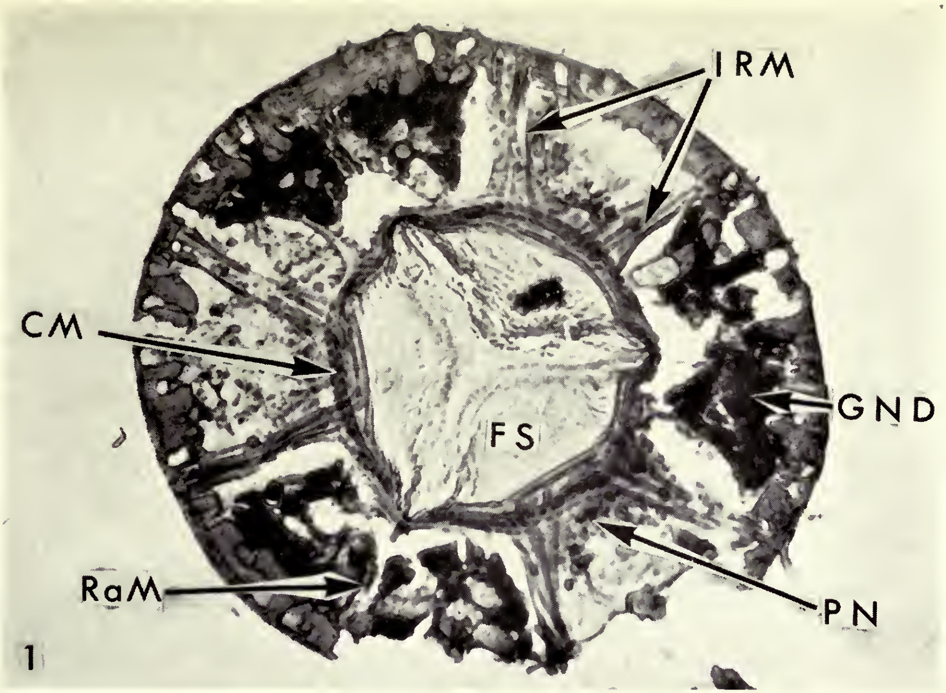

LpM
RaM
IRM
IRM
MPG
MPG
LpM
LpM
2

PLATE 4

Transverse sections of the proboscis of *P. stearnsi*, at levels posterior to those shown in Pl. 3. (Upper) through the proximal third of the proboscis ; (Lower) at a plane immediately anterior to the insertion of the proboscis into the cephalic somite.

See p. 223 for the key to the lettering.


IRM
CM
GND
FS
RaM
PN
1

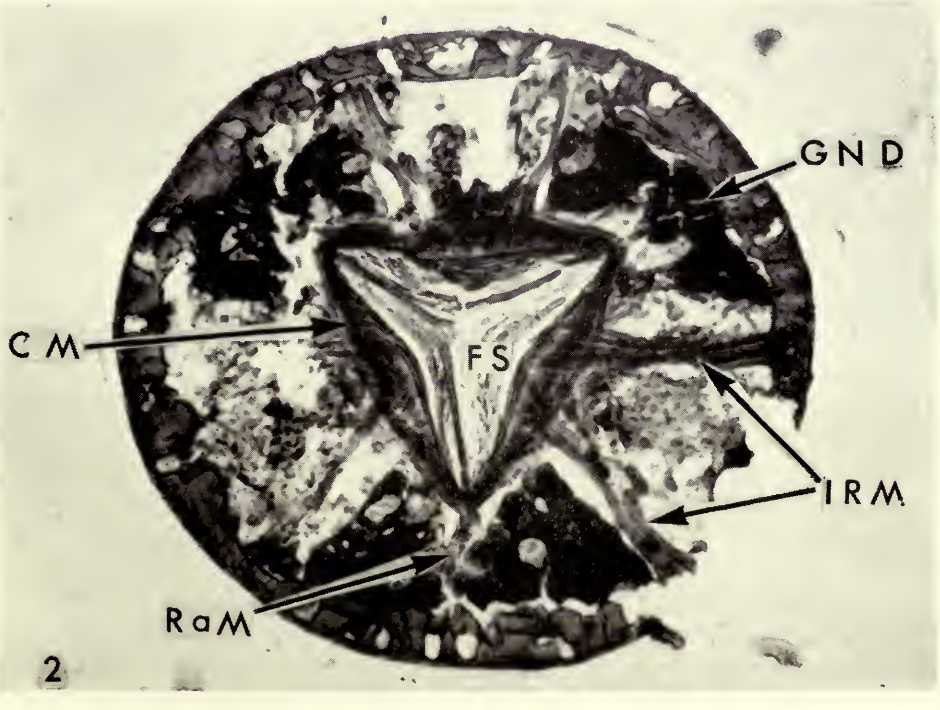
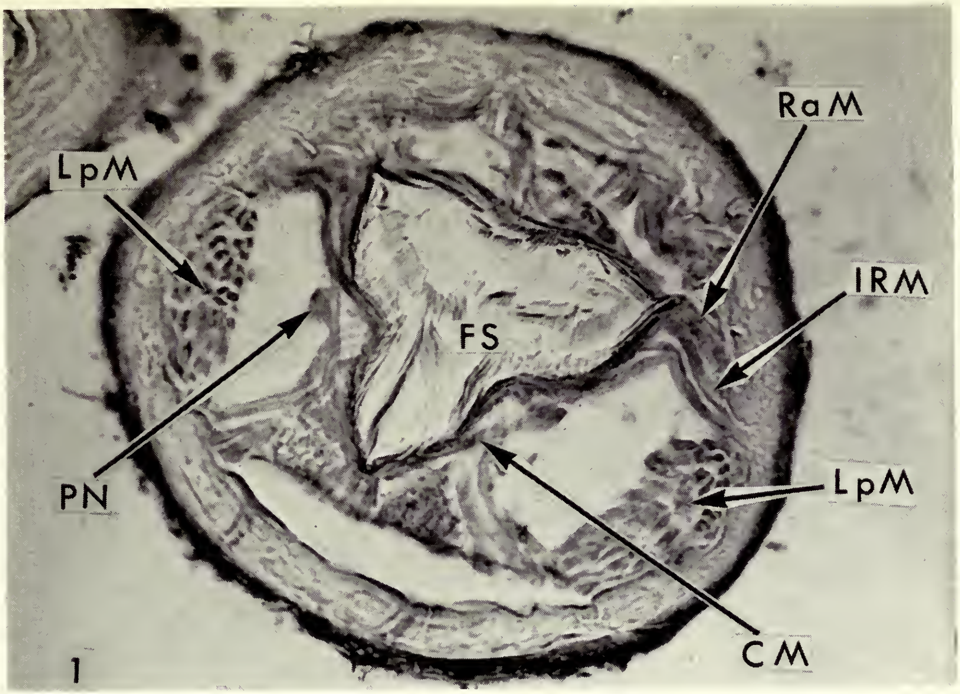
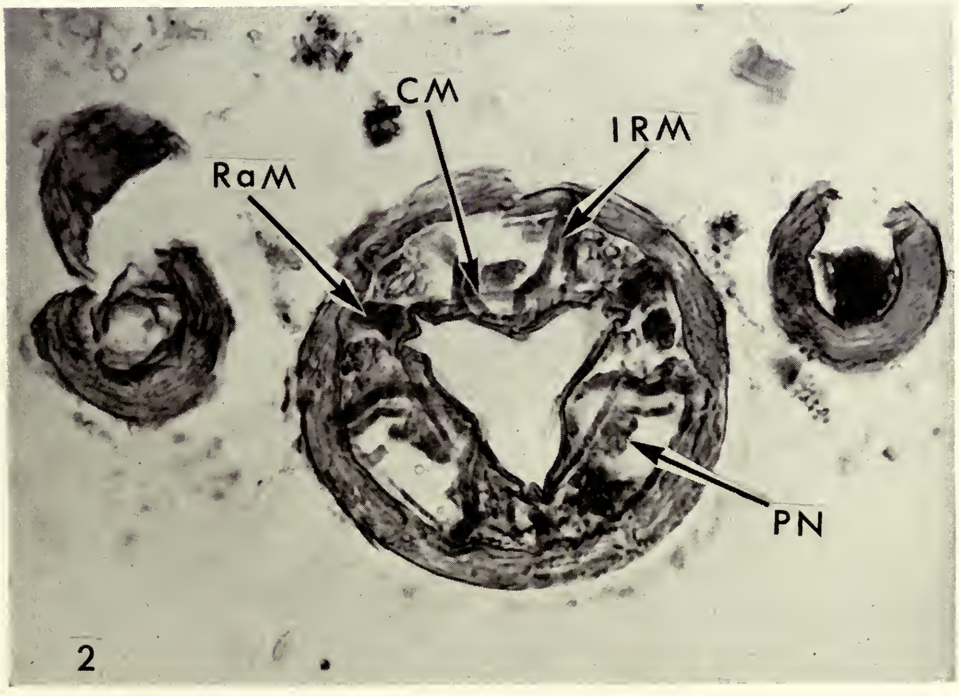

GND
CM
FS
IRM
RaM
2

PLATE 5

(Upper) transverse section of the proboscis of *Rh. australis*, slightly posterior to the midpoint of the proboscis length, showing the presence of lip musculature in the two ventrolateral antimeres only ; (Lower) transverse section through the proximal third of the proboscis of *A. glaciale*.


RaM
LpM
IRM
FS
PN
LpM
CM
1


CM
IRM
RaM
PN
2

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BRITISH MUSEUM
21 JUN 1965
NATURAL HISTORY

P. J. P. WHITEHEAD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 12 No. 7
LONDON: 1965

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21 JUN 1965
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Department of Zoology, British Museum (Natural History)

Pp. 225–281; 4 *Text-figures*

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A REVIEW OF THE ELOPOID AND CLUPEOID FISHES OF THE RED SEA AND ADJACENT REGIONS

By P. J. P. WHITEHEAD

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INTRODUCTION

Fishes of the suborders Elopoidei and Clupeoidei are amongst the most important in world fisheries today. In tropical seas a much greater number of species occur and are exploited than in temperate regions, and biological knowledge of economically important species is often, as a result, hindered by a lack of adequate faunal lists and by problems of systematics. The Red Sea is, in this respect, one of the least studied areas in the Indo-Pacific region, although knowledge of the fishes goes back to the time of Forskål. In his *Descriptiones Animalium*, Forskål (1775) lists four Red Sea species now placed in the suborders Elopoidei and Clupeoidei (*viz. Elops machnata, Albula vulpes, Chirocentrus dorab* and *Thrissina baelama*). The number of such Red Sea species has grown steadily. Rüppell (1837) lists nine, Klunzinger (1871) six, Steindachner (1907) eleven, and Fowler (1956), in the most recent and comprehensive list, includes some thirty-two species (some from the Persian Gulf only). I have here found certain records of only seventeen species

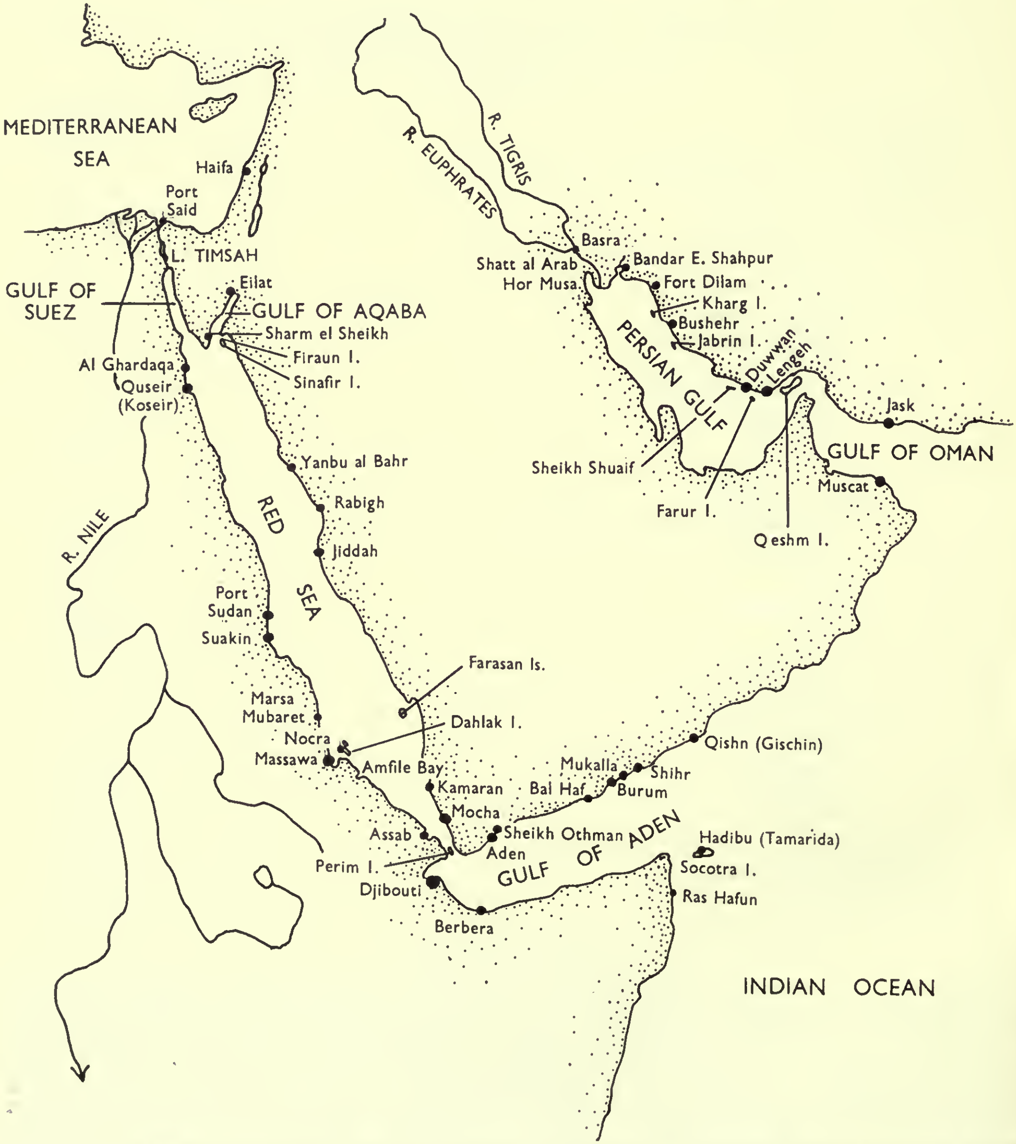
MEDITERRANEAN SEA
Haifa
Port Said
L. TIMSAH
GULF OF SUEZ
Eilat
GULF OF AQABA
Sharm el Sheikh
Firaun I.
Sinafir I.
Al Ghardaqa
Quseir (Koseir)
R. NILE
Yanbu al Bahr
Rabigh
RED SEA
Jiddah
Port Sudan
Suakin
Farasan Is.
Marsa Mubaret
Dahlak I.
Nocra
Massawa
Amfile Bay
Kamaran
Mocha
Assab
Perim I.
Djibouti
Sheikh Othman
Aden
GULF OF ADEN
Berbera
Hadibu (Tamarida)
Socotra I.
Ras Hafun
R. TIGRIS
R. EUPHRATES
Basra
Shatt al Arab
Hor Musa
Bandar E. Shahpur
Fort Dilam
Kharg I.
Bushehr
Jabrin I.
Duwwan
Lengeh
PERSIAN GULF
Jask
GULF OF OMAN
Sheikh Shuaif
Muscat
Farur I.
Qeshm I.
Mukalla
Shihr
Bal Haf
Burum
Qishn (Gischin)
INDIAN OCEAN

FIG. 1. Sketch map of Red Sea and Persian Gulf region. Spelling follows that of the Times Atlas (1959).

from the Red Sea itself, but a further twelve species occur either in the Persian Gulf. the Gulf of Oman, or the Gulf of Aden. Two other species, of Mediterranean origin, are recorded from the Suez Canal.

Collections of Red Sea material are on the whole small, and are scattered amongst a number of museums. It was a pleasure, therefore, to be able to examine, through the courtesy of Professor H. Steinitz, the elopoid and clupeoid material collected by the Israel South Red Sea Expedition (see Oren 1962) deposited at the Hebrew University. In addition, Professor Steinitz kindly offered further Red Sea material collected previous to this, mainly from the Gulf of Aqaba. The list of species represented by these collections was large enough to justify a review of all Red Sea species, and for this reason material has been examined from this museum and borrowed from other institutions. This material includes certain of Rüppell's specimens from the Red Sea, some of Blegvad's (1944) fishes from the Persian Gulf, part of an important and hitherto unrecorded collection made by Fraser-Brunner in the Gulf of Aden, fishes collected by Marshall (1950) in the Gulf of Aqaba, some of Steindachner's Arabian specimens, as well as fishes from smaller collections.

The aim of this review has been to establish the identity of previous records from the Red Sea region in the light of more recent systematic studies than were available to Fowler, and to include material collected since 1956 but for the most part not yet reported on. Even now, there is insufficient material for comparisons to be made between forms from different parts of the Red Sea region ; indeed, only seven species are common to both the Red Sea and the Persian Gulf, and in each case the specimens from the Persian Gulf are too few for a valid comparison to be made. Equally, comparisons between the Red Sea form and the form found in other parts of the Indo-Pacific region are largely limited by poor descriptions relating to the latter area. It is clear, however, that amongst the elopoid and clupeoid fishes, there has been little tendency to endemism in the Red Sea region, and only a single endemic species (from the Gulf of Aden, not from the Red Sea) is recorded here. Almost all the species dealt with here are widespread and, if the Dussumieriidae are any indication, such species can be expected to show very little variation between one region and another. Where, as is usually the case, my material shows no consistent variation from one part of the Red Sea region to another, then I have combined all measurements in a single description of the species.

DESCRIPTIONS, MEASUREMENTS, ETC.

All measurements were made with calipers and are not projected. The following measurements can be commented on.

a. *Standard length* : used throughout.
b. *Head length* : longest possible distance, i.e. not necessarily horizontal.
c. *Snout, eye and postorbital length* : measured along the same horizontal line (through eye centre) and thus *in toto* not equal to head length.
d. *Upper jaw length* : premaxillary symphysis to posterior maxilla tip.
e. *Abdominal scutes* : pre-pelvic counts include the pelvic scute itself, which is the most posterior scute with ascending arms lying in front of the pelvic

fins. The first post-pelvic scute lacks ascending arms and lies between the pelvic fin bases.

The following museum abbreviations have been used :—

H.U. Zoology Department, Hebrew University, Jerusalem (Israel South Red Sea Expedition and other material).
B.M.N.H. British Museum (Natural History).
S.F.R.S. Sea Fisheries Research Station, Haifa.
Z.M.C. Zoological Museum Copenhagen (Blegvad material).
N.M.V. Naturhistorisches Museum, Vienna (Steindachner material).
M.N.H.N. Museum Nationale d'Histoire Naturelle, Paris.
N.-M.F.-I.S. Natur-Museum und Forschungs-Institute, Senkenberg (Rüppell's material).

CLASSIFICATION AND NOMENCLATURE

The system of classification used here differs from that of Fowler (1956) and is based mainly on my own studies (Whitehead, 1963a and unpublished work). Similarly, I have been unable to accept certain of Fowler's names, either as a result of more recent work or of a more thorough examination of specimens and literature. The keys used here employ, where possible, external features suitable for field identification. Vernacular names are taken from Fowler (1956). Synonymies include reference to the original description and to all subsequent records from the Red Sea area (including the Gulf of Aden and the Persian Gulf). The spelling used for place names follows that of the author quoted, but in the section headed Range for each species, and in the map, I have followed the spelling of The Times Atlas (1959 edition).

Key to the Suborders and Families

A Lateral line present on body ; abdominal scutes always absent . Suborder **ELOPOIDEI**
  1 Gular plate present ; 2 supramaxillae . . . . Superfamily ***Elopoidae***
    a. Pseudobranch present ; last dorsal ray not filamentous Family ***Elopidae*** (p. 231)
    b. Pseudobranch absent ; last dorsal ray filamentous Family ***Megalopidae*** (p. 232)
  2 Gular plate reduced or absent ; 1 supramaxilla . Superfamily ***Albuloidae***
    a. Dorsal fin short, about 15 rays . . . . Family ***Albulidae*** (p. 232)
    b. Dorsal fin long, 55–65 rays . . . Family ***Pterothrissidae*** (p. 233)

B Lateral line absent on body ; abdominal scutes often present Suborder **CLUPEOIDEI**
  1 Dorsal much nearer to caudal base than to snout tip ; jaw teeth fang-like Superfamily ***Chirocentroidae***
    A single family, ***Chirocentridae*** (p. 233)
  2 Dorsal origin near midpoint of body ; jaw teeth small or absent (very rarely fang-like) . . . . Superfamily ***Clupeoidae***
    a. Mouth terminal or subterminal, jaws short ; snout not tapering or pig-like.
      i. No abdominal scutes, belly rounded . Family ***Dussumieriidae*** (p. 234)
      ii. Abdominal scutes present, belly usually compressed, keeled Family ***Clupeidae*** (p. 243)
    b. Mouth inferior, jaws long ; snout tapering, pig-like . Family ***Engraulidae*** (p. 263)

Family **ELOPIDAE** (Tenpounders)

ELOPS Linnaeus, 1766

Elops Linnaeus, 1766, *Syst. Nat.*, ed. 12, **1** : 518 (Type : *Elops saurus*).
Argentina Forskål (*part.*), 1775, *Descript. Animal.* : xii, 68.

Revisions : Regan 1909, Bertin 1944a, Whitehead 1962a.

Elops machnata (Forskål)
(Machnat, Shag'oul)

Argentina machnata Forskål, 1775, *Descript. Animal.* : xii, 68 (Djidda).

Elops machnata : Rüppell, 1837,* *Neue Wirlbelth., Fische* : (80) 84 (Red Sea) ; Günther, 1866, *Fishes of Zanzibar* : 121, fig. (caudal) (Red Sea) ; Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116, fig. 2 (Red Sea) ; Bertin, 1944, *C.R. Soc. Biogeograph.* Paris, **21** : 2 (revision, all spp.) ; Fowler, 1956, *Fishes of Red Sea*, **1** : 56 (Indo-Pacific specimens) ; Whitehead, 1962, *Ann. Mag. nat. Hist.*, (13) **5** : 321 (Gulf of Aden).

Elops saurus : Valenciennes, 1846, *Hist. Nat. Poiss.*, **19** : (264) 365 (Red Sea ; Massaua) ; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 470 (Djidda) ; Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 603 (Red Sea) ; Boulenger, 1887, *Proc. zool. Soc. London* : 666 (Muscat) ; Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 167 (S. Arabia).

*Dating follows Sawyer (1952).

DESCRIPTION : based on eight fishes, 110–167 mm. standard length from Sheikh Othman, Gulf of Aden (B.M.N.H. 1962.3.26.1–8).

In percentages of standard length : body depth 17·8–18·8, head length 26·5–29·5 ; snout length 6·1–6·8, eye diameter 6·2–6·9, post-orbital distance 14·7–16·2, upper jaw length 14·9–16·8, lower jaw 15·6–17·2, interorbital 4·3–4·8 ; gular plate, length 9·7–10·1, width 2·5–2·7 ; pectoral length 12·7–14·1, pelvic length 12·7–14·5 ; caudal peduncle, length 14·0–14·9, depth 8·5–9·0, length/depth ratio 1·55–1·70.

Dorsal vi 17–18, pelvic i 16, anal iii–v 11–13 ; scales in lateral series 94–97, scales round caudal peduncle 26 ; branchiostegal rays 29–32 ; vertebrae 63–64.

COLOUR : dorsal surfaces brown, sides silvery. Fins pale brown or colourless.

SIZE : 915 mm. (Fowler).

RANGE : Red Sea (Jiddah, Massawa), Gulf of Aden (Sheikh Othman), Gulf of Oman (Muscat), but apparently not from the Persian Gulf ; elsewhere, Zanzibar, coasts of India, ? S. Africa, East Indies, China, Japan, Hawaii.

E. machnata is distinguished from *E. hawaiensis* Regan by having fewer vertebrae (63–64 ; cf. 68–70) and a longer lower jaw ; and from *E. senegalensis* Regan by its fewer scales (83–97 ; cf. 92–100) (Whitehead 1962a). When further specimens are available, *E. hawaiensis* may prove only subspecifically distinct from *E. machnata*, and the same may be true of *E. senegalensis*. Prof. J. L. B. Smith has sent me a South African specimen which is intermediate between *E. senegalensis* and *E. machnata*.

Specimens:

8 fishes, 111–167 mm., Sheikh Othman, Gulf of Aden (B.M.N.H. 1962.3.26.1-8).

Family **MEGALOPIDAE** (Tarpons)

MEGALOPS Lacepède, 1803

Megalops Lacepède, 1803, *Hist. Nat. Poiss.*, **5** : 289 (Type : *Megalops filamentosus* Lacepède, =*Clupea cyprinoides* Broussonet).

Although *M. cyprinoides* occurs along the East African coast and along the Indian coasts, I can find no record of it in the Red Sea, the Persian Gulf or even in the Gulf of Aden.

Family **ALBULIDAE** (Lady fishes)

Two genera, one of which occurs in the Red Sea.

ALBULA Scopoli, 1777

(Bunnuch, Bunuk, Boenuk, Gasma, Boluk, Bonuk)

Albula Scopoli, 1777, *Introd. Hist. Nat.* : 450 (on Gronow) (Type : *Esox vulpes* Linnaeus).

A single species in all tropical seas.

Albula vulpes (Linnaeus)

Esox vulpes Linnaeus, 1758, *Syst. Nat.*, ed. 10, **1** : 313 (on *Bone Fish* Catesby, 1737, *Hist. Nat. Carolina*, pl. 2, fig. 1—Bahamas).

Albula vulpes : Tortonese, 1937, *Boll. Mus. Zool. Anat. Comp. Univ. Torino*, **45** (3), No. 63 : 12 (Red Sea) ; Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116, fig. 2 (Red Sea) ; *Idem*, 1956, *Fishes of the Red Sea*, **1** : 57 (Indo-Pacific and American specimens).

Argentina glossodonta Forskål, 1775, *Descript. Animal.* : xiii, 68 (Djidda ; Lohaja).

Butirinus glossodontus : Rüppell, 1837, *Neue Wirbelth., Fische* : 80, pl. 20, fig. 2 (Djidda) ; Günther, 1866, *Fishes of Zanzibar* : 120 (Red Sea).

Albula glossodonta ; Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 602 (Red Sea) ; Steinitz & Ben-Tuvia, 1955, *Bull. Sea Fish. Res. Sta., Haifa*. No. 11 : 4 (Gulf of Aqaba).

Argentina bonuk Lacepède, 1803, *Hist. Poiss. Nat.*, **5** : 366 (Arabian Sea).

Albula bananus : Valenciennes, 1846, *Hist. Nat. Poiss.*, **19** (249) 345 (Massaua).

Albula conorhynchus : Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 468 (Red Sea).

DESCRIPTION : based on a single specimen 164 mm., standard length *ex* Aden.

In percentages of standard length : body depth 23·7, head length 28·7 ; snout length 11·3, eye diameter 5·9, interorbital 6·6, upper jaw length 10·5 ; pectoral length 14·7, pelvic length 12·7.

Dorsal iii 14, anal ii 6, pelvic i 9 ; 63 + 6 scales in lateral series ; gillrakers 10 + 1 + 10.

SIZE : 915 mm. (Fowler).

RANGE : Red Sea (Jiddah, Lohaja, Gulf of Aqaba, Massawa), Gulf of Aden (Aden), but not yet from Persian Gulf ; elsewhere, all tropical seas.

On the basis of published material, there seems to be no justification for separating the Red Sea *Albula* from *A. vulpes*, although a world revision with adequate material may demonstrate various subspecies.

Specimens :

1 fish, 164 mm., Aden (B.M.N.H. 1962.3.26 : 9).

1 fish, 374 mm., Red Sea (B.M.N.H. 1845.10.29.71) (stuffed).

1 fish, Gulf of Aqaba, coll. Bertram (H.U. 1699) (not seen).

Günther (1868) lists a half-grown fish, *ex.* Red Sea, but no specimen is labelled as such ; several bottles, however, have no locality data.

Family **PTEROTHRISSIDAE**

Not represented in Red Sea.

Family **CHIROCENTRIDAE** (Wolf Eels)

CHIROCENTRUS Cuvier, 1817

Chirocentrus Cuvier, 1817, *Règne Animal*, **2** : 178 (Type : *Clupea dorab* Forskål).

Fowler (1941) recognises two Indo-Pacific species, one of which occurs in the Red Sea.

Chirocentrus dorab (Forskål)

(Dorab, Lysan, Machnat, Aasa Macha, Abusef, Kharoo, Doheer)

Clupea dorab Forskål, 1775, *Descript. Animal.* : xii, 72 (Djidda ; Moccha).

Chirocentrus dorab : Rüppell, 1837, *Neue Wirbelth., Fische* : 81 (Red Sea) ; Valenciennes, 1846, *Hist. Nat., Poiss.*, **19** : (110) 150, pl. 565 (Massaua) ; Günther, 1866, *Fishes of Zanzibar* : 120 (Red Sea) ; Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 606 (Koseir, Red Sea) ; Boulenger, 1887, *Proc. zool. Soc. London* : 666 (Muscat) ; Meek, 1897, *Field Col. Mus. Publ.*, No. 22, *Zool. Ser.*, **1** (8) : 173 (Aden) ; Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 167 (E. Arabia) ; Tortonese, 1937, *Boll. Mus. Zool. Anat. Comp. Un. Torino*, (3) **45**: 13 (Massaua) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 56, fig. 24 (Bushire Roads); Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116 (Red Sea) ; Ben-Tuvia and Steinitz, 1950, *Bull. Sea Fish. Res. Sta. Haifa*, No. 2 : 4 (Eilat) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 78 (Indo-Pacific specimens) ; Menon, 1960, *Rec. Indian Mus.*, **54** (3–4) : 141 (Persian Gulf).

Description : based on a single specimen 490 mm. standard length from Muscat ; meristic ranges from Fowler (1956).

In percentages of standard length : body depth 14·3, head length 17·4 ; snout length 4·6, eye diameter 3·8, upper jaw length 9·4 ; pectoral length 12·3, pelvic length 2·9 ; pre-dorsal distance 69·5, pre-pelvic distance 49·0, pre-anal distance 67·5.

Canine teeth in jaws. Body strongly compressed, dorsal and anal fins set well behind midpoint of body. Pectoral axillary scales well-developed, about three-quarters length of fin.

Dorsal iv 12–13, pelvic i 6, anal iv 30. No abdominal scutes, but a pair of crescentic pelvic scutes (see Whitehead 1963a). Scales small and caducous ; a scaly sheath at bases of dorsal and anal fins. Gillrakers 3 + 11.

Colour : in alcohol, upper surfaces dark blue or grey, lower surfaces yellow or silvery ; fins hyaline.

Size : 800 mm. (estimated from head length of specimen in Hebrew University) ; Fowler (1956) states " said to reach 12 feet ", but gives no authority for this.

Range : Red Sea (Jiddah, Mocha, Massawa, Quseir, Eilat), Gulf of Aden (Aden), Persian Gulf (Bushehr), Gulf of Oman (Muscat) ; elsewhere, Indian Ocean eastwards to Philippines, China, Australia, Melanesia.

Specimens :

1 fish, 490 mm., Muscat (B.M.N.H. 1887.11.11.321).

1 fish, head only, 139 mm. from premaxillary symphysis, (H.U. no number, no locality but almost certainly Red Sea).

Family **DUSSUMIERIIDAE** (Round herrings)

Fowler (1941, 1956) uses the name Stolephoridae, but this is incorrect (see Opinion 93, *Int. Comm. Zool. Nomenclature*, and Whitehead 1963b and c).

REVISIONS : Bertin 1943a, Whitehead 1963b.

KEY TO THE SUBFAMILIES

A Dorsal rays 16–21 ; branchiostegal rays 14–19 ; adults 150–220 mm. Subfamily ***Dussumieriinae***

B Dorsal rays 11–16 ; branchiostegal rays 6–7 ; adults 50–110 mm. Subfamily ***Spratelloidinae***

Subfamily DUSSUMIERIINAE

Two genera, both found in the Red Sea.

KEY TO THE GENERA

1 Pelvic fins under dorsal base ; two supramaxillae ; anal rays 14–19 . ***Dussumieria***

2 Pelvic fins behind dorsal base ; a single supramaxilla ; anal rays 9–13 ***Etrumeus***

DUSSUMIERIA Valenciennes, 1847

Dussumieria Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 467 (Type : *Dussumieria acuta* Valenciennes).

Montalbiana Bertin (misspelt), 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 7 (Type : *Etrumeus* (*Montalbania*) *albulina* Fowler).

Fowler (1956) recognised two Red Sea species, *D. productissima* Chabanaud as well as *D. acuta* Valenciennes. However, Red Sea specimens of *Dussumieria* closely resemble the Japanese form, and specimens from the Gulf of Aden are intermediate between *D. productissima* and *D. acuta* (Whitehead 1963b). I have therefore recognised only a single Red Sea species, the widespread *D. acuta*.

Dussumieria acuta Valenciennes

(Hashinch (Iran), Mooza, Sardin mabroun, Sardo, Sardin rachidi)

Dussumieria acuta Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 467, pl. 606 (Type locality : Bombay, Coromandel) ; Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 157 (Gischin) 167 (S. Arabia) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 57, fig. 25 (Bushire Roads ; off Jabrin) ; Fowler and Steinitz, 1956, *Bull. Res. Council Israel*, **5** B (3–4) : 261 (Ascalon, E. Mediterranean) ; Fowler, 1956, *Fishes of Red Sea*, **1** : 62 (Indo-Pacific specimens) ; Whitehead, 1963, *Bull. Brit. Mus. nat. Hist.* (*Zool.*), **10** (6) : 312, figs. 1–5 (Gulf of Aden, Persian Gulf, Haifa).

Dussumieria hasseltii : Tillier, 1902, *Mém. Soc. zool. France*, **15** : 318 (Red Sea).

Dussumieria hasselti : Chabanaud, 1932, *Bull. Mus. Hist. nat. Paris*, (2) **4** (7) : 823 (L. Amer.).

Dussumieria productissima Chabanaud, 1933, *Bull. Inst. océanogr. Monaco*, No. 627 : 4, fig. 3 (tongue) and figs. pp. 4–6 (Gulf of Suez ; Lake Timsah) ; *Idem*, 1933, *Bull. Soc. zool. France*, **58** : 289 (Lake Timsah) ; *Idem*, 1934, *Bull. Mus. Hist. nat. Paris*, (2) **6** (1) : 157 (*idem*) ; Gruvel, 1936, *Mém. Inst. Egypte*, **29** : 153, fig. 25 (*idem*) ; Gruvel and Chabanaud, 1937, *loc. cit.*, **35** : 3 (Lake Timsah ; Lake Amer, Suez Canal) ; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 570 (copied) ; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 6, fig. p. 5 (type material) ; *Idem*, 1943, *Bull. Mus. Hist. nat. Paris*, (2) **15** (6) : 390 (Suez Canal ; Gulf of Suez ; Lake Amer) ; Tortonese, 1947, *Hist. nat. Roma*, **2** : 4 (Suez Canal) ; *Idem*, 1948, *Arch. Zool. Ital.*, **33** : 276 (L. Timsah) ; Ben-Tuvia, 1953, *Bull. Sea Fish. Res. Sta., Haifa*, No. 8 : 6, fig. 1 (Haifa, Mediterranean) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 62 (compiled).

DESCRIPTION : based on one fish, 114 mm. standard length from the N. Massawa Channel ; eleven fishes, 105–148 mm., from the Gulf of Aden ; and twenty-five fishes, 64–114 mm., from Haifa. Mediterranean and Gulf of Aden fishes are included in this description because their similarity in morphometric and meristic characters argues that the intervening Red Sea population must also be similar. More Red Sea specimens might show this to be incorrect, however.

In percentages of standard length : body depth 19·3–23·0, head length 25·3–29·4 ; snout length 9·1–10·8, eye diameter 6·9–7·4 ; pre-dorsal distance 55·5–58·5, pre-pelvic distance 60·0–62·5, pre-anal distance 79·0–82·5.

Dorsal iv–v 14–16, pectoral i 12–13 (Haifa only), pelvic i 7, anal ii–iii 12–14 ; gillrakers 26–31 (Chabanaud 29–34) ; branchiostegal rays 14–16.

COLOUR : in alcohol, dorsal surfaces dark blue or dark brown, flanks white or silvery ; fins hyaline.

SIZE : 148 mm. (Gulf of Aden) ; maximum 216 mm. (Day).

RANGE : Eastern Mediterranean (Ben-Tuvia 1953), almost certainly as immigrants from the Red Sea ; Suez Canal, Lakes Timsah and Amer, Gulf of Suez (Chabanaud 1933, Gruvel and Chabanaud 1937) ; Red Sea (Massawa), Gulf of Aden (Mukalla, Shihr, Qishn), Persian Gulf (Jabrin, Bushehr) ; elsewhere, Indo-Pacific region from Natal to Japan.

Specimens :

1 fish, 115 mm., N. Massaua Channel at 27 fathoms (H.U. E57/694).
1 fish, 114 mm., N. Massaua Channel (H.U. E57/732).
5 fishes, 64–114 mm., Haifa, Israel (B.M.N.H. 1962.6.13.4–8).
20 fishes, 77–107 mm., Haifa, Israel (S.F.R.S.).
4 fishes, 102–122 mm., ' Mediterranean ' (H.U. A/16 inv. 2581).
5 fishes, 105–114 mm., Mukalla, Gulf of Aden (B.M.N.H. 1962.3.26.217–221).
6 fishes, 121–148 mm., Shihr & Burum, Gulf of Aden (B.M.N.H. 1962.3.26.211–216).
3 fishes, 89–110 mm., Persian Gulf (Blegvad) (Z.M.C. CN5–7).

NOTES ON MATERIAL EXAMINED : The three Persian Gulf specimens differ from the Red Sea fishes in having slightly deeper bodies (23·4–24·6% of S.L.), shorter snouts (8·2–8·9% of S.L.) and fewer gillrakers (22–24) ; in these characters they resemble Indian Ocean specimens (Whitehead 1963b, figs. 1–3). Chabanaud's (1933) high gillraker counts in Suez specimens are suggestive of a discrete Red Sea population. But the lower counts in Mediterranean specimens hint rather at Phenotypic variation correlated perhaps with temperature or salinity, since the Mediterranean population must have been derived from Red Sea fishes.

ETRUMEUS Bleeker, 1853

Etrumeus Bleeker, 1853, *Verh. Bat. Gen.*, **25** : 48 (Type : *Clupea micropus* Schlegel).

REVISIONS : Bertin 1943a, Whitehead 1963b.

A single, world-wide species chiefly occurring in temperate regions.

Etrumeus teres (De Kay)

(No local names known)

Alosa teres De Kay, 1842, *Nat. Hist. New York*, pt. 4, *Fishes* : 262, pl. 40, fig. 128 (Type locality : New York region).

Etrumeus teres : Whitehead, 1963, *Bull. Brit. Mus. nat. Hist.* (*Zool.*), **10** (6) : 321 (Eilat, Gulf of Aqaba ; Haifa, Mediterranean).

Etrumeus micropus : Fowler and Steinitz, 1956, *Bull. Res. Counc. Israel*, **5**B (3–4) : 261 (except 58 mm. specimen) (Eilat, Gulf of Aqaba).

Note on synonymy.

Although small meristic and proportional differences exist between the various isolated populations of *Etrumeus*, only the South African fishes can be clearly distinguished from the rest (one or two fewer dorsal rays—see Whitehead 1963b). The two Red Sea specimens examined more closely resemble the Japanese rather than the South African form.

DESCRIPTION : based on two fishes, 133–134 mm. standard length from Eilat ; and one fish, 165 mm. from Haifa (its measurements placed in parenthesis).

In percentages of standard length : body depth 16·4–17·1 (20·7), head length 23·7–24·1 (22·8) ; snout length 8·4–8·8 (7·4), eye diameter 8·0–8·2, upper jaw length 8·4 ; pre-dorsal distance 45·0–45·3, pre-pelvic distance 64·5–65·8, pre-anal distance 84·0.

Dorsal v 16 (v 16), pectoral i 15 (i 16), pelvic i 7, anal iii 8 (iii 8) ; gillrakers 32–34 (36). Scales caducous, about 50–56 in lateral series.

COLOUR : in alcohol, dorsal surfaces dark brown or blue, flanks light brown or silver ; fins hyaline.

SIZE : 165 mm. (Haifa) ; maximum 265 mm. (California).

RANGE : Eastern Mediterranean (almost certainly as immigrants from Red Sea), Red Sea (Gulf of Aqaba) ; elsewhere, South Africa ; southern coasts of Australia ; coasts of Japan ; Atlantic and Pacific coasts of North America ; Galapagos Islands.

Specimens :

2 fishes, 133–134 mm., Eilat, Gulf of Aqaba (S.F.R.S. A.339).

1 fish, 165 mm., Haifa, Israel (S.F.R.S. collection).

NOTE ON MATERIAL EXAMINED. The occurrence of *Etrumeus* in the Red Sea is very surprising in view of its distribution elsewhere in warm temperate regions. As in the case of *Dussumieria*, *Etrumeus* is absent from the Eastern Atlantic. It is therefore most likely that the Mediterranean specimen is an immigrant from the Red Sea. Since variation in morphometric and meristic characters between the other, widely distributed populations is slight, the resemblance between the Red Sea fishes and those from Japan is perhaps coincidental (Whitehead 1963b). The great difference in hydrological conditions between these two areas implies considerable morphological stability of the species.

Subfamily SPRATELLOIDINAE

Four Indo-Pacific genera, *Spratelloides*, *Ehirava*, *Gilchristella* and *Spratellomorpha*, of which only the first is represented in the Red Sea area.

SPRATELLOIDES Bleeker, 1851

Spratelloides Bleeker, 1851, *Natuurk. Tijdschr. Ned. Ind.*, **2** : 214 (Type : *Clupea argyrotaeniata* Bleeker = *Clupea gracilis* Schlegel).

Stolephorus : (*non* Lacepède) : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 561.

Some authors have followed Fowler in using *Stolephorus* for this genus, but this is incorrect (see Gosline 1951, Whitehead 1963c).

Two species, both found in the Red Sea.

KEY TO THE SPECIES

a A bright and prominent silver midlateral line ; total anal rays 11–14 ; scales in lateral series 41–49 . . . . ***Spratelloides gracilis***

b No silver band, but whole flank silver ; total anal rays 9–11 ; scales in lateral series 32–46 . . . . ***Spratelloides delicatulus***

Spratelloides gracilis (Schlegel)
(Seil)

Clupea gracilis Schlegel, 1846, *Faun. Japon. Poiss.*, pts. 10–14 : 238, pl. 108, fig. 2 (Type locality: Southeast coasts of Nagasaki).

Spratelloides gracilis : Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 601 (Red Sea) ; Chabanaud, 1932, *Bull. Mus. Hist. nat. Paris*, (2) **4** (No. 7) : 824 (Lac Amer, Suez Canal) ; Gruvel and Chabanaud, 1937, *Mém. Inst. Egypte*, **35** : 4 (Suez Canal) ; Bertin, 1943, *Bull. Mus. Hist. nat. Paris*, (2) **15** (No. 6) : 390 (Gulf of Suez) ; Whitehead, 1963, *Bull. Brit. Mus. nat. Hist. (Zool.)*, **10** (6) : 338, figs. 15–18 (Ghardaqa, Senafir).

Spatelloides (error) *gracilis* : Borsieri, 1904, *Ann. Mus. Civ. Stor. nat. Genova*, (3) **1** : 218 (Nocra, Daalac I., Red Sea).

Stolephorus gracilis : Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116 (Red Sea).

Spratelloides japonicus : Marshall, 1952, *Bull. Brit. Mus. nat. Hist. (Zool.)*, **1** : 22 (Ghardaqa, Senafir).

DESCRIPTION : based on twenty-five fishes, 43·8–54·0 mm., from Eilat, Gulf of Aqaba ; four fishes, 36·0–37·8 mm., from Sinafir, Gulf of Aqaba ; and two fishes, 46·5–48·8 mm., from Ghardaqah.

In percentages of standard length : body depth 13·4–16·8, head length 22·7–24·6 ; snout length 7·2–8·4, eye diameter 5·5–6·6, upper jaw length (from tip of snout) 8·0–9·8 ; pectoral length 10·4–12·1, pelvic length 9·2–10·6 ; pre-dorsal distance 46·4–49·5, pre-pelvic distance 52·0–57·8 ; pre-anal distance (75·2) 79·3–84·0.

Posterior supra-maxilla with upper border rising steeply anteriorly, general shape of expanded portion of this bone as in Figure 2b (see below). Posterior frontal fontanelles divided by wedge of bone anteriorly (Figure 3b) (see below).

Dorsal ii (9) 10, pectoral i 11–12, pelvic i 7, anal (11) 12 of which ii or iii are simple rays. Scales caducous, about 40–50 in lateral series, and 8–9 in transverse series.

COLOUR : in life, upper surfaces pale transparent green with median dorsal line of dark chromatophores ; flank with intense silver band as wide as eye diameter from gill-opening to caudal base, edged above and below by fine irridescent blue line. Lower flank almost transparent, with silver peritoneum visible. Pupil black, iris silver, a small black dot just behind eye. Rest of head silver, with scattered melanophores on tip of lower jaw and snout. A very prominent black mark just above the anterior supra-maxilla. Fins colourless, but black markings at bases of outer caudal rays and along posterior border of caudal peduncle.

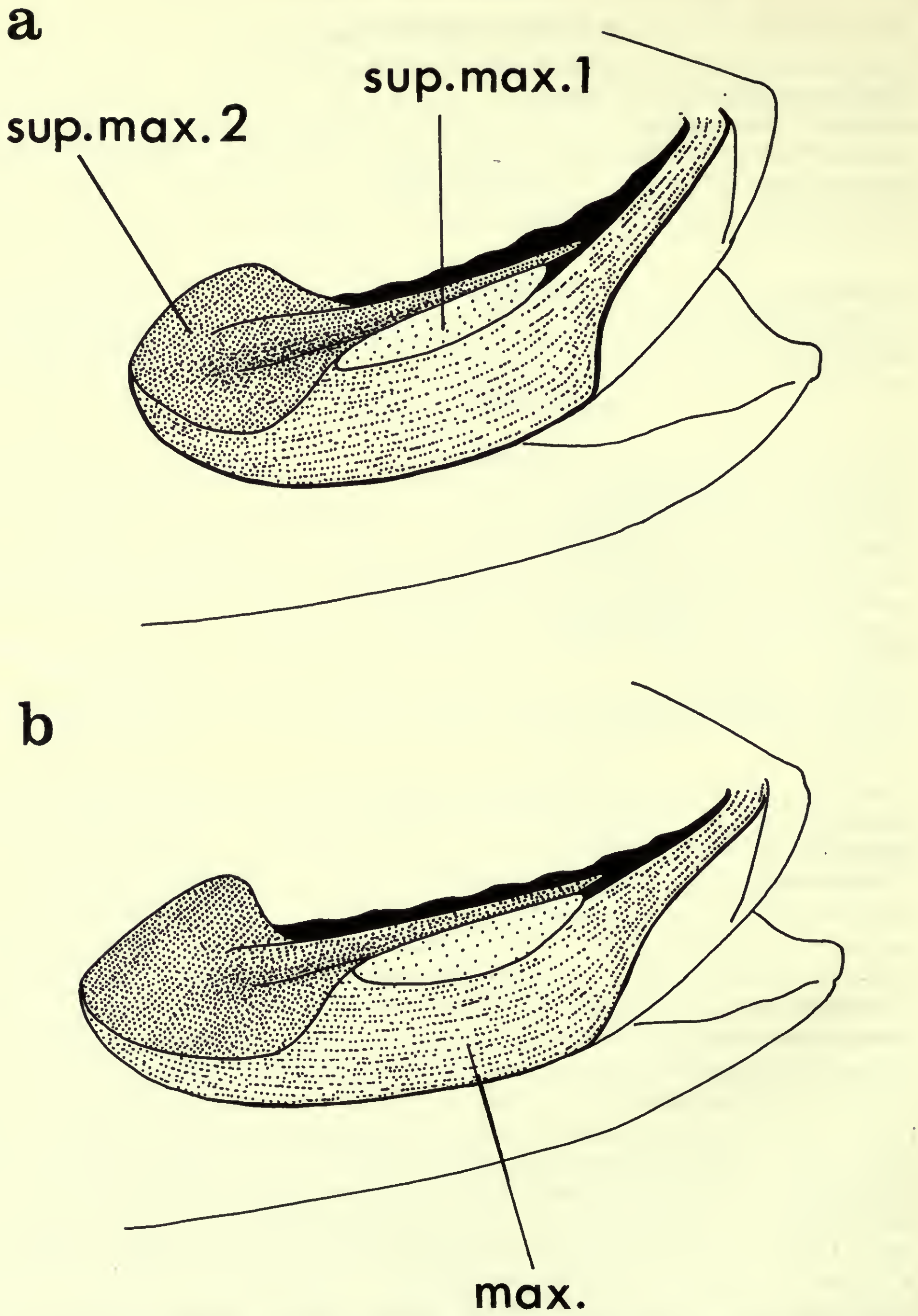

Fig. 2. Maxillary bones in species of *Spratelloides*. a. *S. delicatulus* (42 mm., Red Sea). b. *S. gracilis* (48 mm., Red Sea).
*sup.max.*1 —1st or anterior supra-maxilla. *sup.max.*2 —2nd or posterior supra-maxilla. *max.*—maxilla.

After fixation, silver stripe fades to brown or black, with rest of body light brown, head silver ; all black markings retained.

SIZE : largest specimen examined, 54 mm. S.L. (Japanese specimens up to 93 mm. recorded—Whitehead 1963b, p. 375.)

RANGE : Suez Canal (Lac Amer), Red Sea (Gulf of Suez, Gulf of Aqaba, Sharm el Sheikh, Al Ghardaqah, Sinafir I., Nocra, Dahlak I.), but no records from the Gulf of Aden, Persian Gulf or Gulf of Oman ; elsewhere, widespread in Indo-Pacific region, from East Africa to Japan and Samoa.

Specimens:

2 fishes, 45–47 mm., Ghardaqa, Red Sea (B.M.N.H. 1935.9.30.10–11).
Many fishes, 15–54 mm., Eilat (B.M.N.H. 1963.10.19.51–100).
Many fishes, post-larvae to 37 mm., Sinafir (B.M.N.H. 1951.1.16.36–60).
2 fishes, 12 mm., Eilat (H.U. E55/485, 1).
3 fishes, 18–21 mm., Sharam a Sheikh (H.U. E57/330).
17 fishes, 15–21 mm., Sharam a Sheikh (H.U. E57/329).
Many fishes, 13–15 mm., Eilat (H.U. E56/1).
Many fishes, 13–14 mm., Eilat (H.U. E56/403, 13).
Many fishes, 9–13 mm., Eilat (H.U. E56/403, 11).
15 fishes, 15–19 mm., Sharam a Sheikh (H.U. E57/290).
34 fishes, 10–11 mm., Eilat (H.U. E55/362).
4 fishes, 37–54 mm., Eilat (H.U. E58/303).
5 fishes, 11–17 mm., Eilat (H.U. E58/158, 3).
2 fishes, 17 mm., Eilat (H.U. 2069).
Many fishes, 14–21 mm., Eilat (H.U. E56/403, 14).
6 fishes, 17–21 mm., Sharam a Sheikh (H.U. E57/287).
71 fishes, 16–27 mm., Eilat (H.U. E58/272).
1 fish, 37 mm., Eilat (H.U. E57/678, 1).
1 fish, 29 mm., Eilat (H.U. E58/157d).
51 fishes, 24–29 mm., Eilat (H.U. E49/121).
41 fishes, 25–29 mm., Eilat (H.U. E58/272, 3).
3 fishes, 23–35 mm., Sharam a Sheikh (H.U. E57/325).
3 fishes, 44–46 mm., Eilat (H.U. E60/90, 3).
Many fishes, 18–22 mm., Sharam a Sheikh (S.F.R.S. collection).

NOTES ON MATERIAL EXAMINED. Adults of the two species of *Spratelloides* can be fairly readily separated on colouration and anal finray count. But the Hebrew University collections contain a large number of small juveniles and post-larvae whose identity is difficult to determine. There are, however, three further characters separating the two species which can be applied to fishes of over 20–25 mm.

a. Shape of second (*posterior*) *supra-maxilla.* In *Spratelloides* there are two supra-maxillae, the posterior one being paddle-shaped with a slender anterior shaft. In *S. delicatulus*, the expanded portion of the 2nd supra-maxilla is almost circular, the upper and lower profiles meeting the anterior shaft almost opposite one another. (Figure 2a). In *S. gracilis*, the expanded portion is more oblate, the upper border rises more steeply anteriorly, and the lower profile meets the anterior shaft in front of the point at which the upper border meets it (Figure 2b). This difference in shape also distinguishes the genus *Sardinella* (*delicatulus* shape) from *Herklotsichthys* (*gracilis* shape) (see p. 244).

b. Posterior frontal fontanelles. In *Spratelloides* (but not in *Dussumieria* or *Etrumeus*), a pair of fontanelles on the posterior dorsal part of the head is retained in adults ; the fontanelles are divided in the midline by an anterior extension of the supra-occipital. In *S. gracilis* the fontanelles are longer than in *S. delicatulus*, measuring 1·5–1·8 mm. in fishes over 20 mm. (0·85–1·4 mm. in *S. delicatulus*). A further difference occurs in the shape of the fontanelles (Figure 3a and b). In *S. gracilis* the fontanelles are rather broadly divided anteriorly by a wedge of bone, whereas in *S. delicatulus* they are narrowly divided. This difference also distinguishes the two West Indian species of *Jenkinsia*.

c. Caudal colouration. In both species there are two black markings above and below the midline at the bases of the caudal rays. In *S. delicatulus* these appear as discrete lines of pigment joined at their bases to form a U, whereas in *S. gracilis* they are more diffuse.

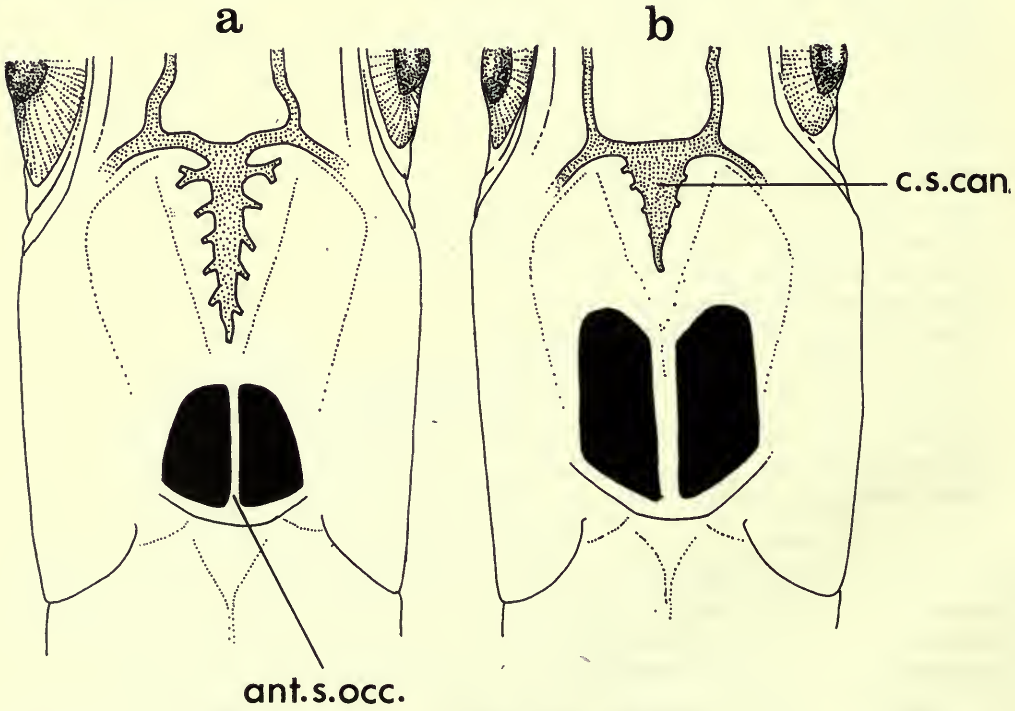

Fig. 3. Dorsal view of posterior part of head showing posterior frontal fontanelle shape (in black) in species of *Spratelloides*. a. *S. delicatulus* (42 mm., Red Sea). b. *S. gracilis* (41 mm., Red Sea).
ant. s. occ.—anterior extension of supra-occipital. *c. s. can.*—cutaneous sensory canal, a posterior extension from the transverse frontal canal.

Spratelloides delicatulus (Bennett)

Clupea delicatula Bennett, 1831, *Proc. zool. Soc. London*, **1** : 168 (type locality Mauritius).
Spratelloides delicatulus : Marshall, 1952, *Bull. Brit. Mus. nat. Hist.* (*Zool.*), **1** : 222 (Gulf of Aqaba) ; Fowler and Steinitz, 1956, *Bull. Res. Counc. Israel*, **5** B (3–4) : 262 (Eilat) ; Whitehead, 1963, *Bull. Brit. Mus. nat. Hist.* (*Zool.*), **10** (6) : 345 (Red Sea, Gulf of Aden).
Etrumeus micropus : Fowler and Steinitz, 1956, *Bull. Res. Counc. Israel*, **5** B (3–4) : 261 (Eilat) (misidentification of 58 mm. specimen).

DESCRIPTION : based on twenty specimens, 38·5–48·5 mm., from Eilat, Gulf of Aqaba ; twelve fishes, 39·1–44·6 mm., from Sinafir ; and three fishes, 38–42 mm., from Marsa Halaib.

In percentages of standard length : body depth 18·4–20·4 , head length 24·2–26·0; snout length 6·4–7·3, eye diameter 6·9–7·9, upper jaw length (from snout tip) 8·9–9·4 ; pectoral length 14·2–15·0, pelvic length 11·8–12·7 ; pre-dorsal distance 45·4–48·5, pre-pelvic distance 53·5–56·0.

Dorsal ii 9–11, pectoral i 10–11, pelvic i 7, anal 9–11 (of which ii or iii are unbranched). Scales caducous, about 32–46 in lateral series, and 7–9 in transverse series.

Posterior supra-maxilla with rounded expanded portion, as in Figure 2a. Posterior frontal fontanelles shorter than in *S. gracilis* and only narrowly divided anteriorly (Figure 3a).

COLOUR : In life, upper surfaces light, vivid blue with dark blue mottling, flanks silver, belly white. Pupil black, iris silver, some small black dots on upper part of operculum. Dorsal part of head dark blue, remainder silver, but tips of snout and lower jaw with dark pigmentation ; a prominent black mark just above anterior supra-maxilla. Fins colourless, but two distinct black lines at base of caudal fin just above and below midline and scattered melanophores along upper border of caudal peduncle.

After fixation, upper surfaces dark brown or black, silver of flanks fading to white ; all black markings retained.

SIZE : largest Red Sea specimen examined, 50 mm. (Australian specimens up to 77 mm.—Whitehead 1963b, p. 376.)

RANGE : Red Sea (Eilat, Sinafir I., Marsa Halaib, Derom I., Nocra, Kad Eidwid reefs), Gulf of Aden, but not from Persian Gulf or Gulf of Oman ; elsewhere, widespread in Indo-Pacific region, from East African coast to Australia (but not to Japan).

Specimens:

10 fishes, 21–49 mm., Firaun I. (B.M.N.H. 1951.1.16.14–23).
12 fishes, 39–47 mm., Senafir I. (B.M.N.H. 1951.1.16.24–35).
16 fishes, 16–45 mm., Marsa Halaib (B.M.N.H. 1960.3.15.16–31).
8 fishes, 36–39 mm., Kad Eidwid reefs (B.M.N.H. 1960.3.15.33–39).
16 fishes, 39–42 mm., Gulf of Aden (B.M.N.H. 1962.6.19.1–16).
1 fish, 40 mm., (alizarin) Marsa Halaib (B.M.N.H. 1960.3.15.32).
Many fishes, 20–30 mm., Eilat (B.M.N.H. 1963.10.19.1–50).

1 fish, 49 mm., Eilat (S.F.R.S. A42/a 1949).
37 fishes, 35–47 mm., Eilat (H.U. E56/408).
37 fishes, 41–49 mm., Eilat (H.U. E?/227).
2 fishes, 42–48 mm., Eilat (H.U. E56/404).
3 fishes, 37–42 mm., Eilat (H.U. E60/70).
35 fishes, 19–42 mm., Derom I. (H.U. E57/770, 3).
8 fishes, 37–48 mm., Eilat (H.U. E56/405).
1 fish, 39 mm., Eilat (H.U. E55/839).
2 fishes, 36–48 mm., Eilat (H.U. E59/176, 1).
3 fishes, 24–47 mm., Eilat (H.U. E58/157d).
2 fishes, 39–47 mm., Eilat (H.U. E58/272, 2).
1 fish, 50 mm., Eilat (H.U. E57/678, 1).
1 fish, 29 mm., no data (H.U. E62/3316).
6 fishes, 35–43 mm., Nocra I. (H.U. E62/587).
11 fishes, 23–36 mm., no data (H.U. E62/3335).
Many fishes, 18–44 mm., no data (H.U. E62/3322).
1 fish, 18 mm., Eilat (H.U. E55/364).
11 fishes, 19–23 mm., Eilat (H.U. E55/524a).

NOTE ON MATERIAL EXAMINED. Where one or two juveniles under 20 mm. occur in a sample of larger fishes, the identity of the juveniles has been presumed to be the same as the larger fishes. In many samples, however, this could not be done, and these are recorded below as *Spratelloides* sp.

In most of the genera of the Dussumieriidae there is only a single abdominal scute, the pelvic scute. In *Spratelloides* the pelvic scute is W-shaped, the arms encircling the bases of the anterior pelvic rays. The pelvic scute was clearly visible in a fish of 21·7 mm., and just visible at 17·5 mm. This ruled out the possibility that the smaller fishes were juvenile clupeids, since the latter have lateral ascending arms on the pelvic scute, and also the pelvic scute (at least in the Pellonulinae) develops after the other abdominal scutes, according to Poll (1964).

Specimens (*Spratelloides* sp. juveniles):
10 fishes, 19–24 mm., Eilat (H.U. E58/158, 4).
1 fish, 21 mm., Eilat (H.U. E55/524f).
1 fish, 17 mm., Eilat (H.U. E55/524g).
19 fishes, 10–18 mm., Eilat (H.U. E57/678, 7).
1 fish, 22 mm., Eilat (H.U. E55/524b).
4 fishes, 20–29 mm., Sharam a Sheikh (H.U. E57/326).
19 fishes, 16–22 mm., Derom I. (H.U. E57/7702).
10 fishes, 14–22 mm., Eilat (H.U. E59/176, 5).
31 fishes, 14–20 mm., Eilat (H.U. E58/268, 1).
2 fishes, 14–15 mm., ? Massawa (H.U. E57/680, 2).
25 fishes, 11–19 mm., Eilat (H.U. E58/272, 5).
7 fishes, 14–17 mm., Derom I. (H.U. E57/770, 1).
10 fishes, 10–16 mm., Khoz Seguri, S. Red Sea (H.U. E61/14, 2.1).

Family **CLUPEIDAE** (Herrings)

Seven genera, representing four of the five subfamilies of the Clupeidae, are found in the Red Sea.

Key to the Genera

A Mouth terminal, sometimes superior ; stomach generally not gizzard-like.
  1 Anal fin moderate, 15–25 rays ; pelvic fins present.
    a. Upper jaw without median notch (Clupeinae)
      i. Fronto-parietal striae few (3–7) ; last two anal rays not enlarged ***Herklotsichthys***
      ii. Fronto-parietal striae many (7–14) ; last two anal rays enlarged ***Sardinella***
    b. Upper jaw with median notch (Alosinae); a single genus . . ***Hilsa***
  2 Anal fin long, more than 30 rays ; lower jaw prominent ; pelvic fins absent or very small. (Pristigasterinae.)
    a. Pelvic fins absent ; anal with 50–63 branched rays . . ***Opisthopterus***
    b. Pelvic fins present ; anal with 34–36 branched rays . . . ***Ilisha***
B Mouth inferior, dentary reflected outwards ; stomach gizzard-like (Dorosomatinae)
  1 Last dorsal ray filamentous . . . . ***Nematalosa***
  2 Last dorsal ray not filamentous . . . . . ***Anodontostoma***

Subfamily Clupeinae

HERKLOTSICHTHYS Whitley, 1951

Herklotsella Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85**: 246 (Type : *Harengula dispilonotus* Bleeker) (*non Herklotsella* Herre 1933, a siluroid genus).
Herklotsichthys Whitley, 1951, *Proc. Roy. zool. Soc. N.S.W.*, 1949–50 : 67 (proposed to replace *Herklotsella* Fowler 1934).
Harengula Valenciennes (*part.* i.e. Indo-Pacific species only), 1847, *Hist. Nat. Poiss.*, **20** : 201 (Type : *Harengula latulus* Valenciennes = *Clupea macropthalma* Ranzani, designated by Gill, 1861, *Proc. Acad. nat. Sci. Philad.*, : 36).

The Indo-Pacific species formerly placed in *Harengula* (e.g. by Fowler 1941) differ from the Western Atlantic species in lacking a small toothed hypo-maxillary bone lying between the tip of the pre-maxilla and the maxilla (Berry, in press). As I have shown elsewhere (Whitehead 1964a), *Clupalosa* Bleeker, *Paralosa* Bleeker and *Wilkesina* Fowler were based on species of *Sardinella*, while *Herklotsella* Fowler is pre-occupied by *Herklotsella* Herre.

The genus *Herklotsichthys* is badly in need of revision. As in *Sardinella*, species are chiefly separated on slight differences in body depth and numbers of gillrakers, both of which, at least in some cases, vary with the size of the individual. Some intraspecific variation in meristic counts may also be correlated with environmental factors or even, as in the case of *Dussumieria* (Whitehead 1963b), show a general increase (or decrease) towards the eastern and western limits of the Indo-Pacific region.

Herklotsichthys closely resembles *Sardinella*, but in addition to the two characters shown in the key above, the two genera can also be separated on the shape of the second (posterior) supramaxilla. In *Herklotsichthys* the lower part of the expanded portion of this bone is larger than the upper part as in *Spratelloides gracilis* (Figure 2b). In *Sardinella,* the upper and lower lobes are about equal in size, the bone being more paddle-shaped, as in *Spratelloides delicatulus* (Figure 2a). However, in *H. vittata* the shape is nearer to the *Sardinella* type although still referable to the *Herklotsichthys* shape.

Key to the Species of Herklotsichthys

1 Gillrakers on lower part of first arch 29–38 ; caudal and dorsal tips colourless or faintly dusky ; dorsal and pectoral usually with 14–15 branched rays **H. punctatus**

2 Gillrakers on lower part of first arch 45–57 ; caudal and dorsal tips black or dark grey ; dorsal and pectoral usually with 12–13 branched rays . . **H. vittatus**

In *H. punctatus* the eye is larger than in *H. vittatus* (8·1–10·3% of S.L. in my material ; *cf.* 7·0–7·7) ; the upper jaw is longer (12·4–15·6 ; *cf.* 9·6–10·8) ; the post-orbital distance shorter (8·6–10·7 ; *cf.* 10·6–11·5) ; and the pectoral and pelvic fins are longer (18·2–21·5 and 12·2–15·0 ; *cf.* 17·0–20·5 and 10·2–11·7).

Herklotsichthys punctatus (Rüppell)

Clupea punctata Rüppell, 1837, *Neue Wirbelth., Fische* : 78, pl. 21, fig. 2 (Red Sea).

Harengula punctata : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : (215) 297 (Massaua) ; Tillier, 1902, *Mém. Soc. zool. France*, **15** : 297 (Suez Canal) ; Norman, 1927, *Trans. zool. Soc. London*, **22** (3) : 378 (Lake Timsah ; Great Bitter Lake ; Suez Canal) ; Chabanaud, 1932, *Bull. Mus. Hist. nat. Paris*, (2) **4** (7) : 823 (L. Amer) ; *Idem*, 1936, *Mém. Inst. Egypte*, **29** : 153 (Suez Canal) ; Gruvel and Chabanaud, 1937, *loc. cit.*, **35** : 3 (Suez Canal) ; Bertin, 1943, *Bull. Mus. Hist. nat. Paris*, (2) **5** (6) : 389 (Southern Suez Canal ; Lac Amer) ; Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116 (Red Sea).

Alosa punctata : Günther, 1866, *Fishes of Zanzibar* : 123 (Aden ; Red Sea).

Clupea quadrimaculata Rüppell, 1837, *Neue Wirbelth., Fische* : 78, pl. 21, fig. 3 (Bay of Massaua) ; Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 601 (Red Sea) ; Tillier, 1902, *Mém. zool. Soc. France*, **15** : 297 (Lac Amer ; Lake Timsah) ; Borsieri, 1904, *Ann. Mus. Civ. Storia nat. Genova*, (3) **1** : 217 (Massaua ; Dissei ; Daalac I.).

Harengula bipunctata Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : (216) 298 (Massaua).

Clupea bipunctata Ehrenberg, in Valenciennes (*loc. cit.*) (name in synonymy).

Harengula arabica Valenciennes, 1847, *op. cit.* : (217) 298 (Mohila).

Clupea arabica Ehrenberg, in Valenciennes (*loc. cit.*) (name in synonymy).

? *Clupea venenosa* : Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 599 (Red Sea) ; Boulenger, 1887, *Proc. zool. Soc. London* : 666 (Muscat) ; Steindachner, 1907, *Denskschr. Akad. Wiss. Wien*, **71** (1) : 157 (Gischin ; Bal Haf ; Ras Schoab, Socotra), p. 167 (S. Arabia).

Clupea mollucensis : Bamber, 1915, *J. Linn. Soc. London*, **31** (Zool.) : 478 (Sudanese Red Sea).

Harengula ovalis : Tortonese, 1947, *Hist. Nat. Roma*, **2** : 4 (Suez Canal) ; Fowler, 1956, *Fishes of the Red Sea* : 64 (on Indo-Pacific specimens).

Sardinella melanura : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 66 (Bender Shahpur ; Bushire) ; Fowler ,1956, *Fishes of the Red Sea*, **1** : 67 (on Blegvad).

Note on synonymy.

Some authors have followed Fowler (1941) in identifying *Clupea ovalis* Bennett with this species. However, it seems unlikely that Bennett (1830) would have chosen this relatively slender species to describe as " *Clup. corpori ovali* " ; *Clupea ovalis* might refer to a species of *Sardinella* (depth 2·8–3·0 times in standard length in *S. bulan*) ; or, in view of the low anal count and black humeral spot described by Bennett, *Hilsa kelee* seems possible. Bennett's description is poor, and the name should perhaps be considered a *nomen dubium*.

Three of Rüppell's paratypes of *Clupea quadrimaculata* which I have examined are clearly *H. punctatus* (gillrakers 34, 36, 36). Valenciennes (1847) based *Harengula bipunctata* on Ehrenberg's notes on " *Clupea bipunctata* ", and similarly, *H. arabica* on " *Clupea arabica* " of Ehrenberg. The descriptions are inadequate, and Valenciennes believed the first species at least to be very close to *H. punctatus*. I have followed Fowler (1956) in placing both these species (but tentatively) in the synonymy of *H. punctatus*. Boulenger's (1887) specimen of *Clupea venenosa* from Muscat belongs in this species, and from the descriptions given, *Clupea venenosa* of Klunzinger is also *H. punctatus*. *Clupea mollucensis* of Bamber has no description, but *Harengula mollucensis* Bleeker 1853 is almost certainly a synonym of *H. punctatus*. (The single Bleeker specimen of *H. mollucensis* in this museum, while probably not the holotype, as was supposed by Günther (1868), is *H. punctatus*). I have been able to examine seven specimens of " *Clupea venenosa* " collected by Steindachner from the Gulf of Aden and the Red Sea (see list of specimens studied). All these fishes are *H. punctatus*.

Bertin (1943b) believed that *H. punctatus* had already penetrated to the Mediterranean, basing this on the single record of *Clupea venulosa* Steinitz from the coast of Israel (Steinitz 1927). I have been able to examine this specimen, which is in the collections of the Zoologiczne Museum at Wroclaw (Poland), and it is *Sardinella aurita*. Although part of the collection at Wroclaw suffered damage during the war, Dr. Kozikowska informs me (*in. litt.*) that both the locality and the name labels for this specimen are in the handwriting of Dr. Steinitz.

DESCRIPTION : based on the holotype (58·5 mm.) and two paratypes of *Clupea punctata* Rüppell, 58–61 mm., from the Red Sea ; three paratypes of *Clupea quadrimaculata* Rüppell, 57–82 mm., from the Bay of Massawa ; nine fishes, 63–72 mm., from Eilat ; two fishes, 93–96 mm., from Eilat ; fifteen fishes, 63–73 mm., from Harmil I. (S. Red Sea) ; and four fishes, 82–86 mm., from Candala, Gulf of Aden. Additional head and body depth measurements and scute and gillraker counts made on eight further specimens from the Red Sea (see list of specimens).

In percentages of standard length : body depth 22·8–32·0, head length 25·6–31·4 ; snout length 7·4–8·8, eye diameter 8·1–10·3, upper jaw length 12·4–14·7(15·6), post-orbital distance 8·6–10·7 ; pectoral length 18·2–21·5, pelvic length 12·2–15·0 ; pre-dorsal distance 43·2–49·4, pre-pelvic distance 52·0–58·3, pre-anal distance (74·5)76·2–83·5.

Dorsal iv 14–15, pectoral i 14–15 (16), pelvic i 7, anal ii–iii 13–16 (total (16) 17–19). Abdominal scutes, pre-pelvic 17–18, post-pelvic 11–13 (14), total 28–31 (32). Scales fairly caducous, about 40–45 in lateral series, 10–11 in transverse series. Gillrakers on lower part of first arch 29–38.

Gillrakers

	29	*30*	*31*	*32*	*33*	*34*	*35*	*36*	*37*	*38*	*Mean*
Red Sea . .				2	1	7	13	11	2	1	35·08
Gulf of Aden .			1		1	2					33·00
Persian Gulf .	1		1			1	1				32·25

Branchiostegal rays 6–7.

COLOUR : in alcohol, dorsal surfaces dark grey-blue or brown, flanks silvery or light brown; a series of small black dots on back from dorsal to caudal.

SIZE : 96 mm. (Eilat) ; to 153 mm. (Fowler 1956).

RANGE : Suez Canal (Lakes Timsah and Amer), Red Sea (Eilat, Massawa, Farasan I., Kameran, Suez, Suakim, Quseir, Mersa Haleib, Hassani, Dahlak I., Khoz Seguri, Harmil I., Dissei), Gulf of Aden (Aden, Kandala, Bal Haf, Ras Shoab, Qishn, Socotra), Persian Gulf (Bandar e Shahpur, Bushehr), Gulf of Oman (Muscat); elsewhere, widespread in Indo-Pacific region, from East Africa to Japan, Australia, Polynesia.

Specimens:

1 fish, 58·5 mm., Red Sea, HOLOTYPE of *Clupea punctata* Rüppell (N.-M.F.-I.S. 567).

2 fishes, 58–61 mm., Red Sea, PARATYPES *Clupea punctata* Rüppell (N.-M.F.-I.S. 6649–50).

3 fishes, 57–82 mm., Bay of Massawa, PARATYPES *Clupea quadrimaculata* Rüppell (N.-M.F.-I.S. 4648, 4649, 4651).

4 fishes, 82–86 mm., Eritrea (S.F.R.S. BT699).

1 fish, 68 mm., Khoz Seguri (S.F.R.S. BT676).

19 fishes, 54–71 mm., Massawa (H.U. E56/406).

1 fish, 81 mm., Eilat (H.U. E53/6).

19 fishes, 61–74 mm., Harmil I. (H.U. E62/3327).

2 fishes, 93–96 mm., Eilat (H.U. E56/405).

9 fishes, 63–72 mm., Eilat (H.U. E54/17).

2 fishes, 76–87 mm., Sudan, Red Sea (B.M.N.H. 1963.11.12.2).

1 fish, 89 mm., Muscat (Boulenger's *Clupea venenosa*) (B.M.N.H. 1887.11.11.317).

2 fishes, 67–73 mm., Red Sea, coll. Klunzinger (B.M.N.H. 1871.7.15.27).

4 fishes, 63–77 mm., Persian Gulf (Blegvad's *Sardinella melanura*) (Z.M.C. CN 1–4).

12 fishes, 75–104 mm., Gischin and Red Sea (Hassani, Mersa Haleib, Kosseir, Suakim, Suez, Cameran), Steindachner's *C. venenosa* (N.M.V. 1658, 1663, 1671, 1678, 1681, 1692, 1698).

40 fishes, 45–58 mm., Farasan I., Sarad Sarso, coll. Klausewitz (N.-M.F.-I.S. 4647).

6 fishes, 56–65 mm., Makauwa, Red Sea, coll. Klausewitz (N.-M.F.-I.S. no number).

39 fishes, 61–76 mm., Harmil I. (H.U. E62/3293).

52 fishes, 57–66 mm., Harmil I. (H.U. E62/3294).

19 fishes, 70–74 mm., Goliath Bay (H.U. E62/3252).

Herklotsichthys vittatus (Valenciennes)

Clupeonia vittata Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 352 (Type locality : Vanikoro).
Clupea kowal : Rüppell, 1837, *Neue Wirbelth., Fische* : 79 (Djidda, Massaua) ; ? Giglioli, 1888, *Ann. Mus. Civ. Stor. nat. Genova*, (6) **2** : 72 (Assab).
? *Harengula kowal* : Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116 (? on Rüppell).
? *Kowala coval*: Tortonese, 1947, *Boll. Soc. Adriat. Sci. nat. Trieste*, **43** : 82 (? on Rüppell).

Note on synonymy.

Records of *Kowala* from the Red Sea area seem to have originated from Rüppell's misidentification. Rüppell's specimen has eight pelvic rays (seven in *Kowala*) and a bilobed dermal outgrowth on the vertical portion of the cleithrum (absent in *Kowala:* see Whitehead, 1964c). In meristic and proportional characters, Rüppell's specimen agrees with *H. vittatus*. *Harengula kowal* of Fowler (1945) and *Kowala coval* of Tortonese (1947) are cited without descriptions and were probably based on Rüppell's record, as also *Clupea kowal* of Giglioli (1888).

Günther (1868) included *C. kowal* Rüppell in his synonymy of *Clupea kowal*, but all Günther's specimens (of which Bleeker's type of *Clupalosa bulan* is one) are *Sardinella bulan*. One of these specimens is the Zanzibar *Alosa kowal* of Günther (1866). Three further specimens, not included in the Catalogue but evidently identified by Günther as *Clupea kowal*, are in fact *S. bulan*.

Steinitz (1927) recorded " *Clupea kowal* Günther (*nec* Klunzinger) " from Haifa, Israel. Bertin (1943b) acknowledged this to be an immigrant from the Red Sea but identified Steinitz's specimen with *Sardinella gibbosa* (i.e. *S. jussieu*). I have examined a specimen, now in the collections of the Zoologiczne Museum at Wroclaw in Poland, which is believed to be that described by Steinitz ; it is in fact *Clupea harengus* L. Although the present specimen is the correct length (121 mm. S.L.), the body is too slender to fit Steinitz's description (4·85 times in length ; cf. 3·6 times) and there are fewer anal rays (iii 14 ; cf. 19). From the description, it is not possible to identify Steinitz's *C. kowal* with certainty.

A further reference to *Clupea kowal* is that of Klunzinger (1871). It was not collected by Klunzinger from the Red Sea and the description may have been based on several sources. The body depth is given as 4½–5 times in length, which is too slender for *S. bulan* or *H. vittatus*, but might apply to *S. jussieu* or *S. fimbriata*. *Harengula bulan* of Fowler (1956) and of Tortonese (1947) were based on Klunzinger's *Clupea kowal*. I have omitted all three references from the synonymies.

It seems likely that the genus *Kowala*, known otherwise from India and eastwards to China, is not present in the Western Indian Ocean, all previous records having been based on species of *Herklotsichthys* or *Sardinella*.

K. albella Valenciennes, the type of the genus *Kowala*, is a species of *Sardinella* ; however, *Escualosa* Whitley, 1940, was based on the second of Valenciennes' species, *K. thoracata*, and therefore replaces the name *Kowala* for that species (Whitehead 1964c).

DESCRIPTION : based on sixteen fishes, 75–101 mm., from Alayu (Gulf of Aden) ; and Rüppell's specimen of *Clupea kowal* from the Red Sea.

In percentages of standard length : body depth 27·7–31·2, head length 25·7–27·8 ;

snout length (6·6) 7·1–7·8, eye diameter 7·0–7·7, post-orbital distance 10·6–11·5, upper jaw length 9·6–10·8 ; pectoral length 17·0–20·5, pelvic length 10·2–11·7 ; pre-dorsal distance 44·7–49·2, pre-pelvic distance 53·0–55·2, pre-anal distance 77·0–79·1.

Fronto-parietal striae more irregular and numerous than in *H. punctatus*, about 5–7. Second supra-maxilla smaller than in *H. punctatus* and nearer to the *Sardinella* shape, i.e. lower part of expanded portion only slightly larger than upper part.

Dorsal iv–v (11) 12–15, pectoral i 12–13 (14), pelvic i 7, anal ii–iii (15) 16–17 (total 18–20). Abdominal scutes, pre-pelvic 16–17, post-pelvic 12–13, total (28) 29–30. Scales caducous 40–42 in lateral series (Regan). Gillrakers on lower part of first arch 45–57, increasing with size of fish (46 in a 65 mm. fish, 50 at 80 mm., 57 at 101 mm.).

COLOUR : in alcohol, dorsal surfaces dark, flanks paler, or silvery. Distinguished from *H. punctatus* by black or dark brown caudal tips, visible in most specimens.

SIZE : 101 mm. (Gulf of Aden).

RANGE : Red Sea (Jiddah, Massawa, i.e. Rüppell's *Clupea kowal* records), Gulf of Aden (Alayu, Ras Antara), but no records from the Persian Gulf or Gulf of Oman ; elsewhere, Indian Ocean from Red Sea to East Indies, also Philippines, Melanesia, Micronesia, Polynesia.

Specimens:

40 fishes, 65–101 mm., Alayu (surf cast-net) (B.M.N.H. 1962.3.26.160–199).
2 fishes, 32–33 mm., Ras Antara (B.M.N.H. 1962.3.26.200–201).
1 fish, 77 mm., Rüppell's *Clupea kowal*, Red Sea (N.-M.F.-I.S. SMF 560).

Rüppell's *C. kowal*, the only Red Sea specimen of *H. vittatus*, differs from the Gulf of Aden fishes in having slightly more branched rays in the dorsal and the pectoral fins (15 and 14 ; cf 12–13 and 12–13 respectively) ; in this respect it approaches *H. punctatus*, but it has more gillrakers (55).

SARDINELLA Valenciennes, 1847

Sardinella Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 28 (Type : *Sardinella aurita* Valenciennes, designated by Gill, 1861, *Proc. Acad. nat. Sci. Philad.* : 35).

Clupeonia Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 345 (Type : *Clupanodon jussieu* Lacepède, designated by Gill, *op. cit.* : 35).

Kowala Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 362 (Type : *K. albella* Valenciennes = *Sardinella brachysoma* Bleeker—see Whitehead 1964c).

Amblygaster Bleeker, 1849, *J. Ind. Arch.*, **3** : 73 (Type : *Amblygaster clupeoides* Bleeker = *Clupea sirm* Walbaum—see Bertin 1944b).

Clupalosa Bleeker, 1849, *Verh. Bat. Gen.*, **22** : 12 (Type : *Clupalosa bulan* Bleeker—see note below).

Paralosa Bleeker, 1868, *Versl. Akad. Amst.*, **2** (2) : 300 (Type : *Harengula* (*Paralosa*) *valenciennesi* = *Sardinella melanura* (Cuvier)—see note below).

Wilkesina Fowler & Bean, 1923, *Proc. U.S. nat. Mus.*, **63** : 3 (Type : *Harengula fijiense* Fowler & Bean = *Sardinella nymphaea* (Richardson)—see note below).

Note on synonymy.

The names *Kowala, Clupalosa, Paralosa* and *Wilkesina* have been added to this synonymy as a result of examination of type material (Whitehead 1964a, c).

Some authors (e.g. Bertin 1944b) favour splitting *Sardinella* into three subgenera : *Sardinella* (for *S. aurita* and *S. longiceps*), *Amblygaster* (for *S. sirm* and *S. leiogaster*) and *Clupeonia* (for the remaining species). The genus is, however, badly in need of revision and I have preferred to ignore these subgeneric divisions for the time being.

The species of *Sardinella* are distinguished chiefly by differences in gillraker count and body depth. Study of material from the whole Indo-Pacific region may well reduce several species to subspecies or mere geographical forms. Fowler (1956) lists nine Red Sea or Persian Gulf species. I have recognised six species from this area, of which only three, *S. sirm, S. jussieu* and *S. fimbriata*, are definitely known from the Red Sea itself.

KEY TO THE SPECIES OF SARDINELLA

A Abdominal scutes keeled and well-exposed.
  1 Pelvic rays 9 ; dark spot on upper angle of operculum ; gillrakers 180–250 **S. longiceps**
  2 Pelvic rays 8 ; dark spot often at base of unbranched dorsal rays ; gillrakers less than 180.
    a. Gillrakers 45–57 ; body deep, 33–36% of S.L. **S. bulan (= S. perforata auct.)**
    b. Gillrakers 70–166 ; body variable, 24–34% of S.L. . . **S. maderensis**
    c. Gillrakers 53–72 ; body slender, 23–31% of S.L.
      i. Gillrakers 53–58 (at 97–114 mm. S.L.) ; snout 6·4–7·3% of S.L. **S. jussieu**
      ii. Gillrakers 60–72 (at 87–118 mm. S.L.) ; snout 7·3–8·0% of S.L. **S. fimbriata**
B Abdominal scutes feebly keeled, barely exposed, belly smooth ; gillrakers 38–45 **S. sirm**

Sardinella longiceps Valenciennes

Sardinella longiceps Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : (198) 273 (Type locality : Pondicherry) ; Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 379 (Muscat) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 65 (Indo-Pacific specimens).

Clupea longiceps : Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 167 (E. Arabia).

Clupea scombrina : Boulenger, 1887, *Proc. zool. Soc. London* : 666 (Muscat).

DESCRIPTION : based on twenty-five fishes, 79–136 mm., from Aden and Abyan (no Red Sea material).

In percentages of standard length : body depth 22·1–24·7, head length 30·0–33·8 ; snout length 7·5–8·7, eye diameter 6·0–7·6 (8·2), postorbital length 13·3–16·0, upper jaw length 11·8–12·9 ; pectoral length 16·2–17·9, pelvic length 9·0–9·9 ; pre-dorsal distance 46·0–50·0, pre-pelvic distance 53·5–59·0, pre-anal distance 78·0–82·0 (84·0).

Dorsal iv–v 13–14 (15), pectoral i 13–16, pelvic i 8, anal ii–iii 12–14 (total 15–16). Abdominal scutes, pre-pelvic (17) 18–19 (20), post-pelvic 13–15, total 32–33 (34). Scales caducous, 46 or 47 in lateral series (Fowler). Gillrakers fine, numerous, 180–250 on lower part of first arch (Regan).

COLOUR : in alcohol, dorsal surfaces dark, flanks silver, fins colourless except dark fringe to anal.

LENGTH : 136 mm. (Gulf of Aden) ; 166 mm. (Fowler, 1956).

RANGE : Gulf of Aden (Aden, Abo, Ruqub, Abyan, Ras Antara), Gulf of Oman (Muscat), but no records from either the Red Sea or the Persian Gulf ; elsewhere, Indian Ocean and eastwards to Indonesia and Philippines (see Li 1960). *S. longiceps* replaces *S. aurita* in the Indian Ocean, but their ranges seem to overlap in Indonesia and the Philippines. No evidence that *S. aurita* from the Mediterranean has passed through the Suez Canal.

Specimens:

14 fishes, 79–101 mm., Aden (B.M.N.H. 1962.3.26.49–62).
7 fishes, 82–111 mm., Gulf of Aden (B.M.N.H. 1962.3.26.89–95).
1 fish, 142 mm., Abo, Somaliland (B.M.N.H. 1962.3.26.69).
12 fishes, 88 + 130–135 mm., Gulf of Aden (B.M.N.H. 1962.3.26.37–48).
9 fishes, 115–135 mm., Ruqub (B.M.N.H. 1962.3.26.10–18).
19 fishes, 123–136 mm., Abyan, Gulf of Aden (B.M.N.H. 1962.3.26.70–88).
6 fishes, 19–21 mm., Ras Antara, Somaliland (B.M.N.H. 1962.3.26.63–68).
3 fishes, 106–115 mm., Muscat, Arabia (Boulenger's *Clupea scombrina*) (B.M.N.H. 1887.11.11.314–316).

Sardinella bulan (Bleeker)

Hashinch, Moomagh (Iran)

Clupalosa bulan Bleeker, 1849, *Verh. Bat. Gen.*, **22** : 12 (Madura Strait, Kammal and Surabaya, Java).

Clupea (*Harengula*) *perforata* : Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 158 (Gischin).

Clupea perforata : Steindachner, *loc. cit.* : 167 (S. Arabia).

Sardinella perforata : Tortonese, 1934, *Boll. Mus. Zool. Anat. comp. Torino*, **44** (3) No. 49 : 5, fig. 1 (Persian Gulf) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 64 (N.W. of Jask ; S. Duwwan) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 65 (Indo-Pacific specimens).

Note on synonymy.

Regan (1917) placed *Clupalosa bulan* Bleeker and *Spratella kowala* Bleeker in the synonymy of *S. perforata* Cantor. Re-examination of the probable Bleeker holotypes of those two species (Whitehead 1964a) has shown that Regan correctly identified the two Bleeker specimens. However, Bleeker's *bulan* (1849) has priority over Cantor's *perforata* (1850) and should be used for this species (Whitehead 1964c).

DESCRIPTION : based on three fishes, 87–99 mm., from Ruqub (Gulf of Aden) ; two fishes, 89–90 mm., from the Gulf of Aden ; one fish, 77 mm., from Abyan ; and seven fishes, 74–97 mm., from the Persian Gulf.

In percentages of standard length : body depth 31·2–35·5, head length 24·8–27·0 ; snout length 5·8–6·7, eye diameter 7·1–8·4, post-orbital length (7·6) 8·6–9·6, upper jaw length 10·3–11·5 ; pectoral length 19·1–21·2, pelvic length 10·5–12·9 ; pre-dorsal distance 43·0–46·6, pre-pelvic distance 52·0–55·8 (57·0) pre-anal distance 77·0–82·5 (85·0).

Dorsal iv 14–15, pectoral i (13) 14, pelvic i 7, anal iii 17–19. Abdominal scutes, pre-pelvic 18, post-pelvic 12–13 (14), total 30–31 (32). Scales in lateral series 37–41 (Fowler). Gillrakers on lower part of the first arch 47–54 (57) ; a slight indication that higher counts may occur in Gulf of Aden than in Persian Gulf fishes (independent of size).

	Gillrakers										
	47	*48*	*49*	*50*	*51*	*52*	*53*	*54*	*55*	*56*	*57*
Gulf of Aden . .		2	1	1				1			1
Persian Gulf . .	1		2			2	1				

Colour : in alcohol, upper surfaces dark brown, flanks silvery or paler brown. A dark spot at bases of unbranched dorsal rays and tips of these rays dusky, otherwise fins colourless. In some fishes the caudal tips appear faintly dusky.

Length : 99 mm. (Gulf of Aden) ; 143 mm. (Fowler).

Range : No Red Sea records, but known from Gulf of Aden (Qishn, Ruqub, Abyan), Persian Gulf (Duwwan) and Gulf of Oman (Jask) ; elsewhere, recorded (as *S. perforata*) from the East Indies, Philippines, Siam, Amoy, Polynesia. The only Indian Ocean record appears to be *Clupea kowal* Günther 1868 (Zanzibar, a skin) ; I have now examined further examples of this species from Zanzibar.

Specimens:

3 fishes, 87–99 mm., Ruqub, Gulf of Aden (B.M.N.H. 1962.3.26.96–98).
2 fishes, 89–90 mm., Gulf of Aden (B.M.N.H. 1962.3.26.99–100).
1 fish, 77 mm., Abyan, Gulf of Aden (B.M.N.H. 1962.3.26.101).
4 fishes, 91–97 mm., N.W. of Jask and S. of Duwwan. (Blegvad's *S. perforata*, Z.M.C. CN 8–11).
3 fishes, 74–80 mm., Persian Gulf (B.M.N.H. 1869.3.4.31–33).

Sardinella maderensis (Lowe)

Clupea maderensis Lowe, 1836, *Trans. zool. Soc. London*, **2** (3) : 189 (Type locality : Madeira).

Harengula maderensis : Jordan and Hubbs, 1917, *Ann. Carnegie Mus.*, **9** (3–4) : 461 (Port Said).

Sardinella maderensis : Chabanaud, 1933, *Bull. Soc. zool. France*, **58** : 288 (L. Timsah, Suez Canal) ; *Idem*, 1934, *Bull. Mus. Hist. nat. Paris*, (2) **6** (1) : 156 (*idem*) ; Gruvel, 1936, *Mém. Inst. Egypte*, **29** : 152 (Suez Canal) ; Gruvel and Chabanaud, 1937, *loc. cit.*, **35** : 2, fig. 2 (Port Said ; L. Amer, Suez Canal) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 66 (Canaries, Syria).

Sardinella (*Clupeonia*) *maderensis* : Bertin, 1943, *Bull. Mus. Hist. nat. Paris*, (2) **15** (6) : 388 (L. Timsah, L. Amer).

Sardinella (*Clupea*) *granigera* : Tillier, 1902, *Mém. Soc. zool. France*, **15** : 295 (L. Timsah).

Harengula granigera : Fowler, 1923, *Proc. Acad. nat. Sci. Philad.*, **75** : 35 (Beirut, Syria).

Sardinella eba : Norman, 1927, *Trans. zool. Soc. London*, **22** (3) : 376 (L. Timsah) ; Chabanaud, 1932, *Bull. Mus. Hist. nat. Paris*, (2) **4** (7) : 832 (L. Amer).

Clupea (*Sardinella*) *eba* : Gruvel, 1936, *Mém. Inst. Egypte*, **29** : 152 (L. Timsah ; L. Amer.)

Note on synonymy.

Ben-Tuvia (1959) concluded that only differences in body depth separate the types of *S. maderensis*, *S. eba* (Valenciennes), *S. granigera* (Valenciennes) and *S. cameronensis* Regan ; and that body depth is too variable a character on which to base these species. However, Tortonese (1961) believed that *S. maderensis* and *S. granigera* are distinct, but he placed *S. eba* in the synonymy of the latter.

DESCRIPTION : based on Ben-Tuvia (1959), but proportional measurements converted to percentages.

In percentages of standard length ; body depth 24·4–34·5 (see also Ben-Tuvia 1959, Table 1), head length 22·2–29·5 ; pre-dorsal distance 40·0–47·5, pre-pelvic distance 45·5–55·5, pre-anal distance 66·5–91·0 ; distance pectoral to pelvic 23·2–30·3, distance pelvic to anal 21·2–27·0. In percentages of head length : snout 23·8–31·2, eye diameter 22·2–32·2, interorbital width 17·3–25·7, maxilla length 33·3–47·5 ; pectoral length 55·5–83·0, pelvic length 34·5–47·5.

Dorsal 17–21, pectoral i 13–i 16, pelvic i 7, anal 17–22. Abdominal scutes, pre-pelvic 18–20, post-pelvic 13–15, total 31–34. Scales in lateral series 40–50. Gillrakers 70–166 in fishes over 60 mm., increasing with size of fish.

COLOUR : " (fresh) : back grey-blue, sides and belly silvery. Top of head and tip of snout dark. Cheeks and opercular region silvery white with blue-green irridescence. A dark diffused blotch behind the upper hind border of the branchial opening. Immediately posterior to this blotch, a narrow golden band stretches along the body to the caudal fin, parallel to the fourth or fifth row of scales. Additional golden streaks less distinct and narrower run parallel above and below this band. Dorsal fin dusky yellow with a black spot at the base of the first five rays. Anal and ventrals whitish. Pectorals dusky. Caudal fin dusky, becoming darker towards the tips ". (Ben-Tuvia 1959).

LENGTH : up to 275 mm. (Ben-Tuvia 1959).

RANGE : Port Said, Suez Canal, L. Timsah, L. Amer, but not recorded from Gulf of Suez or Red Sea ; elsewhere, Mediterranean, Eastern Atlantic (Madeira, Cameroons).

Specimens :

1 fish, 127 mm., L. Timsah (B.M.N.H. 1925.9.19.4).

2 fishes, 69–71 mm., between Port Said and Damietta (B.M.N.H. 1928.11.30. 1–2).

Sardinella jussieu (Lacepède)

Clupanodon jussieu Lacepède, 1803, *Hist. Nat. Poiss.*, **5** : 469, 474, pl. 11, fig. 2 (Type locality : Mauritius).

Sardinella jussieu : Fowler, 1941, *Fishes of the Red Sea*, **1** : 67 (Indo-Pacific specimens).

Clupea fimbriata : Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 158 (Gischin, S. Arabia).

Harengula dollfusi Chabanaud, 1933, *Bull. Inst. océanogr. Monaco*, No. 627 : 1, fig. 1 (gillraker, tongue), fig. 2, scale (Gulf of Suez) ; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 600 (compiled) ; Tortonese, 1947, *Boll. Soc. Adriat. Sci. nat. Trieste*, **43** : 82 (compiled).

Sardinella (*Clupeonia*) *gibbosa* : Bertin, 1943, *Bull. Mus. Hist. nat. Paris*, (2) **15** (6) : 389 (Suez Canal ; Gulf of Suez).
Sardinella sindensis : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 65 (Gulf of Oman).

Note on synonymy.

Regan (1917) and some later authors have rather doubtfully identified *Clupanodon jussieu* Lacepède with this species and have preferred to use Bleeker's name *gibbosa* instead. Valenciennes (1847) claimed to have examined specimens similar to those of Commerson (Lacepède's description was based on Commerson's notes), and he notes that the operculum shows " *stries rayonnantes, fines et nombreuses* ". In no species of either *Sardinella* or *Harengula*, however, is the operculum striated ; the appearance of striae can be given by the much branched cephalic sensory canal system on the operculum, but this is common in both genera and would hardly call for comment. Valenciennes (*loc. cit.* p. 349) described a second species, *Clupeonia fasciata*, which he believed almost identical to his *C. jussieu* but lacking the opercular striae, and with two less anal rays. The description of *C. fasciata* agrees well with the present species, and Fowler (1941) placed it in the synonymy of *Sardinella jussieu*. It has priority over *S. gibbosa* (Bleeker), 1849, and should be used if *Clupanodon jussieu* Lacepède should prove to be a *nomen dubium*.

I have not examined specimens of *Harengula dollfusi* but have accepted Bertin's (1943b) synonymy ; Dr. M. Blanc has been unable to locate these types in the Museum National d'Histoire Naturelle.

S. sindensis (Day) differs from *S. jussieu* in having slightly more gillrakers (58–62 ; *cf.* 50–55 (Fowler), 53–57 in my material). Blegvad's single specimen of *S. sindensis* has 55 gillrakers. *S. sindensis* can perhaps be considered a synonym of *S. jussieu*, representing an eastern form or subspecies.

Description : based on six fishes, 97–114 mm., from Mukalla ; four fishes, 99–115 mm., from Mukalla ; and one fish, 119 mm., from the Gulf of Oman (Blegvad's *S. sindensis*).

In percentages of standard length : body depth 24·3–27·4, head length 24·3–26·9 ; snout length (6·4) 6·9–7·3, eye diameter (6·3) 6·6–7·5, post-orbital (8·6) 9·3–10·1, upper jaw length 9·4–10·8 ; pectoral length (16·4) 17·6–18·0, pelvic length (8·8) 9·9–10·4 ; pre-dorsal distance 42·5–47·6, pre-pelvic distance 48·8–54·0, pre-anal distance 78·3–81·5.

Dorsal iv 14–15, pectoral i 13–14, pelvic i 7, anal iii (14) 15–17. Abdominal scutes, pre-pelvic (17) 18 (19), post-pelvic (14) 15, total 32–33 (34). Scales caducous, 40–42 in lateral series (Fowler).

Gillrakers 53 (f.2) 54 (4) 55 (5) 56 (1) 57 (2), mean 54·88.

Colour: in alcohol, upper surfaces grey/blue or dark brown, flanks silvery or pale brown. A prominent dark spot at bases of unbranched dorsal rays, otherwise fins colourless.

Length : 119 mm. (Gulf of Oman) ; 178 mm. (Fowler).

RANGE : Suez Canal, Red Sea (Gulf of Suez), Gulf of Aden (Mukalla, Qishm, Aden), Gulf of Oman, but not recorded from the Persian Gulf ; elsewhere, Indian Ocean from Mauritius to East Indies, and from China, Australia, Micronesia, Polynesia.

Specimens :

6 fishes, 97–114 mm., Mukalla (B.M.N.H. 1962.3.26.102–107).
6 fishes, 99–115 mm., Mukalla (B.M.N.H. 1962.3.26.111–116).
3 fishes, 54–58 mm., Aden (B.M.N.H. 1962.3.26.108–110).
1 fish, 119 mm., Gulf of Oman (Z.M.C. C1—Blegvad's *S. sindensis*).
2 fishes, 118–119 mm., Gischin, coll. Hein (N.M.V. 1260).

Sardinella fimbriata (Valenciennes)

Sefer, Hashinch, Moomagh (Iran)

Spratella fimbriata Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : (263) 359, pl. 601 (Type locality : Malabar).

Sardinella fimbriata : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 65, fig. 29 (copied Day) (off Fort Dilam) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 66 (on Philippine specimens).

Note on synonymy.

Bertin (1944b), after an examination of the Valenciennes types of *Clupeonia jussieui* and *Spratella fimbriata*, concluded that the two represented a single species, which he believed to have " environ 70 branchiospines à la branche inférieure du premier arc branchial ". But, until the validity and identity of Lacepède's *C. jussieu* can be definitely confirmed or rejected, it seems best to retain the name *fimbriata* for the material described here.

S. jussieu (as understood here, i.e. *sensu* Fowler, 1941, 1956) very closely resembles *S. fimbriata*. Dutt (1961a, 1962), who studied the two species off the Waltair Coast of India, stated that *S. fimbriata* makes its appearance there earlier than *S. gibbosa* (i.e. *S. jussieu*), but that at times when the two species coincide, their shoals are almost always discrete (Dutt 1962). He distinguished the two species on gillraker counts which, although increasing slightly with size of fish, remain just distinct (a difference of 2, 2, 3, 6, 6, 5, 8, 5, 2, 4, 0, 4 rakers respectively in the 10 mm. groups 30–140 mm. standard length).

In my material (24 fishes, 87–118 mm.) I have assigned specimens with a count of 53–58 rakers to *S. jussieu*, and those with 60–72 rakers to *S. fimbriata*. In this size range, Dutt's ranges in gillraker counts are respectively 43–60 and 57–77, with average values of 48, 52, 53, 56 for *S. jussieu* and 63, 66, 69, 70 for *S. fimbriata* in the 10 mm. groups represented (mean values of 54·9 and 66·5 respectively in my material).

In the specimens examined here, there are no other meristic differences between the two species, and proportional measurements are almost identical except for a slightly shorter snout in *S. jussieu* (6·4–7·3 per cent. of S.L. ; cf. (6·7) 7·3–8·0 in *S. fimbriata*). Fowler (1956) finds a difference in numbers of scales in lateral series, *S. fimbriata* having a lower count (36–38 ; cf. 40–42), but counts are not always possible or perhaps accurate in these fishes.

Both species have now been recorded from the Persian Gulf area (the record of *S. jussieu* being based solely on Blegvad's Gulf of Oman specimen of *S. sindensis*) ; *S. jussieu* is now recorded from the Gulf of Aden and the Red Sea (as *H. dollfusi*), while *S. fimbriata* is recorded from the Red Sea but not the Gulf of Aden. Gillraker counts within these localities are still consistent with the hypothesis that two species are present in the area.

Numbers of rakers

	Red Sea	Gulf of Aden	Persian Gulf area
S. jussieu	53–56 (Chabanaud 1933)	53–57 (12)	55 (1) (Gulf of Oman)
S. fimbriata	60, 62 (2)	—	60–72 (20)

In conclusion, it can be said that Regan's (1917a) Indian specimens of *S. fimbriata* had counts of 70–75 rakers, while Fowler's (1941) Philippine specimens had 80 rakers. Such variations in number of rakers may further complicate the distinction between the two species, and the problem cannot be resolved on the basis of such small samples as the present one.

Description : based on twenty fishes, 87–118 mm., from the Persian Gulf ; two fishes, 114–115 mm., from off Fort Dilam, Persian Gulf (Blegvad's specimens of *S. fimbriata*), and two fishes, 93–101 mm., southern Red Sea.

In percentages of standard length : body depth 23·0–25·4 (27·6–29·8), head length 25·2–27·8 ; snout length (6·7) 7·3–8·0, eye diameter 6·5–7·6, post-orbital distance 9·0–10·6, upper jaw length 9·9–11·1 ; pectoral length 16·1–18·9, pelvic length 8·8–10·4 ; pre-dorsal distance 43·3–47·2 ; pre-pelvic distance 49·2–54·8, pre-anal distance 77·0–80·5.

Dorsal iv 14–15 (16), pectoral i 13–15, pelvic i 7, anal ii–iii 15–17 (total 17–20). Abdominal scutes, pre-pelvic (17) 18, post-pelvic 14–15 (16), total 32–33 (34). Scales caducous, 36–38 in lateral series (Fowler). Gillrakers, 60 (f. 4), 61 (1), 62 (1), 63 (2), 64 (2), 65 (4), 66 (3), 67 (1), 68 (2), 69 (1) and 70 (1), mean 64·75 (72 in one fish).

Colour : in alcohol, upper surfaces dark blue/grey or dark brown, flanks silvery or pale brown. A faint dark spot at bases of unbranched dorsal rays (as in *S. jussieu*), otherwise fins colourless (" caudal tip dark "—Fowler 1956).

Length : 118 mm. (Persian Gulf) ; 135 mm. (Philippines—Fowler).

Range : Persian Gulf (off Fort Dilam), and from Red Sea (North of Mt. Guba) ; elsewhere, Indian Ocean (India to East Indies), Philippines, China.

Specimens :

41 fishes, 87–118 mm., Persian Gulf (B.M.N.H. 1962.10.20.1–41).
2 fishes, 114–115 mm., off Fort Dilam, Persian Gulf (Z.M.C. CN 2 and 3, Blegvad's *S. fimbriata*).
1 fish, 102 mm., S. Red Sea (H.U. E58/305).
1 fish, 94 mm., north of Mt. Guba, Red Sea (H.U. E57/715).

Sardinella sirm (Walbaum)
(Aenab.)

Clupea sirm Walbaum, 1792, *Artedi Pisc.*, **3** : 38 (on Forskål, 1775, *Descript. Animal.* 17—Arabia) ; Rüppell, 1837, *Neue Wirbelth., Fische* : 77, pl. 21, fig. 1 (Massaua) ; Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 598 (Red Sea).

Alosa sirm : Günther, 1866, *Fishes of Zanzibar* : 123 (Red Sea).

Sardinella sirm : Tortonese, 1935, *Boll. Mus. Zool. Anat. Comp. Un. Torino*, ser. 3, **45** (6) : 13, fig. 1 (scale) (Massaua) ; Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116, fig. 2 (Red Sea) ; Tortonese, 1947, *Boll. Soc. Adriat. Sci. nat. Trieste*, **43** : 82 (Massaua).

Sardinella (*Amblygaster*) *sirm* : Bertin, 1943, *Bull. Mus. Hist. nat. Paris*, ser. 2, **15** (6) : 389 (Gulf of Suez).

Clupea liogaster : Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 598 (Kosier, Red Sea) ; Steindachner, 1871, *Denkschr. Wiss. Wien*, **71** (1) : 158 (Makalla ; Gulf of Aden), 167 (S. Arabia).

Sardinella leiogaster : Tortonese, 1947, *Boll. Soc. Adriat. Sci. nat. Trieste*, **43** : 82 (Red Sea).

Harengula bipunctata Ehrenberg : in Klunzinger, *loc. cit.* : 599 (name in synonymy).

? *Sardinella clupeoides* : Fowler, (*part.*), 1941, *Bull. U.S. nat. Mus.*, No. 100 : 619 (Red Sea specimen only) ; Tortonese, 1947, *Boll. Soc. Adriat. Sci. nat. Trieste*, **43** : 82 (on Fowler) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 68 (on Fowler 1941).

Note on synonymy.

Fowler (1941) records " 32? " gillrakers in a single specimen from the Red Sea, and places this specimen in *S. clupeoides* (Bleeker). Since this is only 5 rakers less than the lowest recorded here for *S. sirm*, and since *Amblygaster clupeoides* Bleeker, 1849, was described from the East Indies, it seems possible that Fowler's count was incorrect. Gillraker numbers may increase with size of fish, but Fowler's specimen was large enough (126 mm.) to have an adult count. Tortonese (1947) followed Fowler in listing *S. clupeoides* for the Red Sea. Bertin (1944b), having examined type material, claimed that *S. leiogaster* Valenciennes 1847, is identical to and has priority over *S. clupeoides* ; hitherto, authors (e.g. Regan 1917) have placed *S. leiogaster* in the synonymy of *S. sirm*.

DESCRIPTION : based on two fishes, 129–147 mm., from Massawa (collected by Rüppell) ; four fishes, 105–126 mm., from Mukalla, Gulf of Aden ; one fish, 120 mm., from Abo, Somaliland ; and one fish, 109 mm., from Eritrea.

In percentages of standard length : body depth 19·4–24·3, head length 24·0–26·2 ; snout length 7·1–8·8, eye diameter 6·0–7·2, upper jaw length 8·9–9·8, post-orbital distance 8·6–9·5 ; pectoral length 14·3–17·0, pelvic length 8·5–9·9 ; pre-dorsal distance 44·2–46·2, pre-pelvic distance 49·4–53·0, pre-anal distance 78·4–81·0.

Abdominal scutes present, but with very poorly developed keels so that belly feels smooth.

Dorsal iv 14–15, pectoral i 15–16, pelvic i 7, anal ii or iii 15–16 (total 18–19). Abdominal scutes, pre-pelvic 17–18, post-pelvic 14–15, total 31–33. Scales caducous, 42–45 in lateral series (Regan). Gillrakers, 38 (1), 39 (1), 40 (1), 41 (1), 42 (3), 45 (1) on lower part of first arch ; only 35 gillrakers in a 63 mm. specimen from Zanzibar.

COLOUR : in alcohol, upper surfaces grey-blue or dark brown, flanks silvery, fins colourless.

SIZE : 147 mm. (Massawa) ; up to 280 mm. (Fowler 1956).

RANGE : Red Sea (Massawa, Gulf of Suez, Quseir, Shab Sheikh), Gulf of Aden (Abo, Mukalla), but not from the Persian Gulf or Gulf of Oman ; elsewhere, Indian Ocean (Zanzibar to East Indies), Philippines, China, Micronesia, Polynesia.

Specimens :

4 fishes, 105–126 mm., Mukalla (B.M.N.H. 1962.3.26.119–122).
1 fish, 120 mm., Abo, Somaliland (B.M.N.H. 1962.3.26.118).
1 fish, 109 mm., Shab Sheikh, Eritrea (from stomach of *Euthynnus affinis*) (H.U. E57/690).
2 fishes, 129–147 mm., Massaua, Rüppell's specimens (N.-M.F.-I.S. 458).

Subfamily ALOSINAE

Of the two Indo-Pacific alosinid genera, *Hilsa* and *Gudusia*, only the former is represented in the Red Sea area. There is as yet no record of *Hilsa* from the Red Sea itself, only from the Persian Gulf and the Gulf of Aden. Since *H. ilisha* (and probably *H. kelee* also) spawns in rivers, it is unlikely that anything more than stray individuals can be expected in the Red Sea. In the Persian Gulf, on the other hand, shoals of *H. ilisha* ascend the Tigris and Euphrates (Mahdi 1962).

H. kelee differs from all other species in several respects and can be placed in a separate subgenus (Whitehead, 1965).

Revisions : Regan (1917), Whitehead (1965).

KEY TO THE SUBGENERA

1 Fronto-parietal region with numerous exposed striae ; no pectoral axillary scale ; expanded portion of maxilla with several longitudinal ridges . . subgenus ***Hilsa***

2 Fronto-parietal region covered with thick skin, few or no striae ; pectoral axillary scale present ; expanded portion of maxilla smooth or with fine striae subgenus ***Tenualosa***

HILSA Regan, 1917

Paralosa Regan (*non Paralosa* Bleeker), 1916, *Ann. Durban Mus.*, **1** : 167 (Type : *Clupea durbanensis* Regan).

Hilsa Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 303 (Type : *Clupea durbanensis* Regan).

Tenualosa Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 (Type : *Alosa reevesii* Richardson).

Macrura Fowler, (*non Macrura* van Hasselt), 1941, *Bull. U.S. nat. Mus.*, No. 100 : 626 (Type : *Clupea kelee* Cuvier).

Subgenus ***Hilsa***

Hilsa kelee (Cuvier)

Clupea kelee Cuvier, 1829, *Règne Animal*, ed. 2, **2** : 320 (name in footnote, based on *Keelee* Russell, 1803, *Fishes of Coromandel*, **2** : 75, pl. 195—Type locality : Vizagapaṭam).

Macrura kelee : Fowler, 1956, *Fishes of the Red Sea*, **1** : 69 (Indo-Pacific specimens).

Hilsa kelee : Whitehead, 1965, *Bull. Brit. Mus. nat. Hist.* (*Zool.*), **12** (4): 129 (Gulf of Aden and Indo-Pacific specimens).

Alosa chapra : Günther, 1866, *Fishes of Zanzibar* : 123 (Aden) (misidentification).

Hilsa kanagurta : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 63 (N. of Farur).

Note on synonymy.

As I have shown elsewhere (Whitehead 1965), Fowler (1941) was mistaken in using van Hasselt's name *Macrura* in a generic sense.

DESCRIPTION : based on four fishes, 129·2–133·2 mm., from Aden ; and two fishes, 80·2–90·0 mm., from Jibuti.

In percentages of standard length : body depth 37·4–41·5, head length 33·0–36·1 ; snout length 7·5–8·5, eye diameter 8·3–9·5, upper jaw length (from snout tip) 14·3–16·4 ; pectoral length 20·4–21·0, pelvic length 10·9–12·0 ; pre-dorsal distance 47·5–50·5, pre-pelvic distance 54·5–57·5 ; operculum height 18·2–20·6, width 8·6–10·0. Fronto-parietal area exposed, striated (as in *Sardinella*). Expanded portion of maxilla with several longitudinal ridges. No pectoral axillary scale.

Dorsal iv 13–14, pelvic i 7, anal iii 18–19. Abdominal scutes, pre-pelvic 16, post-pelvic 13, total 29.

COLOUR : in alcohol, back and upper part of head brown, flanks silvery. A dark humeral blotch, followed (in some specimens) by seven or eight black blotches. Tips of anterior dorsal rays dusky, as also caudal tips.

LENGTH : Aden specimens up to 133 mm. (South African specimens up to 180 mm.).

RANGE : Persian Gulf (Farur) and Gulf of Aden (Aden, Djibuti), but no records from Red Sea itself ; elsewhere, Western Indo-Pacific region from Natal to Burma and Siam.

Specimens :

4 fishes, 129–133 mm., Aden (B.M.N.H. 1962.3.26.202–205).
5 fishes, 65–91 mm., Jibuti (B.M.N.H. 1962.3.26.206–210).

Subgenus ***Tenualosa***

Hilsa ilisha (Hamilton-Buchanan)

Clupanodon ilisha Hamilton-Buchanan, 1822, *Fishes of the Ganges* : 243, 382, pl. 19, fig. 73 (Type material from : Ganges estuaries ; Patua ; Goyakarra ; Calcutta ; Dhasa).
Clupea ilisha : Day, 1878, *Fishes of India*, pt. 4 : 640, pl. 172, fig. 3 (Tigris).
Hilsa ilisha : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 306 (Persian Gulf, Burma) ; Hora & Misra, 1943, *J. Roy. Asiatic Soc. Bengal*, **9** : 2 (Persian Gulf ?) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 63, fig. 28 (photo) (Bushire) ; Menon, 1960, *Rec. Indian Mus.*, **54** (3–4) : 141 (Habanian) ; Mahdi, 1962, *Fishes of Iraq* : 11 (Tigris, Euphrates) ; Khalaf, 1962, *Mar. f-water fishes of Iraq* : 17 (Persian Gulf) ; Whitehead, 1965, *Bull. Brit. Mus. nat. Hist.* (*Zool.*), **12** (4) : 134 (Tigris, Basra, and Indian specimens).
Macrura ilisha : Fowler, 1956, *Fishes of the Red Sea*, **1** : 69 (copied from Regan).

DESCRIPTION : based on three fishes, 100–127 mm., from Basra ; and three fishes, 115–131 mm., from the Tigris ; no Red Sea material.

In percentages of standard length : body depth 31·0–36·0, head length 28·6–32·5 ; snout length 6·6–7·0, eye diameter 6·0–7·1, upper jaw length 12·3–14·5 ; operculum, height 14·4–15·7, width 7·5–9·2 ; pre-dorsal distance 47·8–49·5, pre-pelvic distance 51·5–53·5 ; caudal length 33·2 (one fish only).

Fronto-parietal area covered by thick skin, no striae but sometimes one or two lateral ridges. Expanded portion of maxilla smooth. Pectoral axillary scale present.

Dorsal iv or v 15–16, pectoral i 13–15, pelvic i 7, anal iii 17–18. Abdominal scutes, pre-pelvic (16) 17, post-pelvic 14–15, total (30) 31–32.

LENGTH : largest specimen examined 360 mm. ; Mahdi (1962) gives 250–350 mm. and Khalaf (1962) 400 mm., but it is not indicated whether this applies to Iraq fishes. Elsewhere, fishes of up to 600 mm. (females) have been recorded (Chacko and Ganapati 1949).

RANGE : Persian Gulf (Tigris, Euphrates, Basra, Bushehr) but no Gulf of Aden or Red Sea records ; elsewhere, Indian Ocean eastwards to Burma and Cochin China.

BIONOMICS, FISHERY, ETC. : a full review of the fisheries and existing knowledge concerning this species has been published recently (Pillay and Rosa 1963).

Specimens. 3 fishes, 115–131 mm., Tigris (B.M.N.H. 1875.1.14.11–13). 6 fishes, 99–127 mm., Basra (B.M.N.H. 1920.3.3.178–182). (Dry specimens). 1 fish, 350 mm., Tigris (B.M.N.H. 1875.1.14.14). 1 fish, 360 mm., Tigris (B.M.N.H. 1875.1.14.15).

Subfamily PRISTIGASTERINAE

OPISTHOPTERUS Gill, 1861

Opisthopterus Gill, 1861, *Proc. Acad. nat. Sci. Philad.* : 38 (Type : *Pristigaster tartoor* Valenciennes).

A single species in this area.

Opisthopterus tardoore (Cuvier)

Pristigaster tardoore Cuvier, 1829, *Règne Animal*, ed. 2, **2** : 321 (on *Tartoore* Russell, 1803, *Fishes of Coromandel*, **2** : 74, pl. 103 : Vizagapatam).
Opisthopterus tardoore : Fowler, 1956, *Fishes of the Red Sea*, **1** : 70 (Indo-Pacific specimens).
Opisthopterus tartus : Zugmayer, 1913, *Abhandl. Bayer. Akad. Wiss.*, **26** (6) : 9 (Oman).
Opisthopterus indicus : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 68, fig. 31 (copied Day) (off Jask).

DESCRIPTION : based on a single fish, 136 mm., Blegvad's specimen from near Jask, Gulf of Oman.

In percentages of standard length : body depth 31·5, head length 21·2 ; snout length 5·2, eye diameter 6·5, upper jaw length 12·0, lower jaw length 10·8 ; pectoral length 23·5 ; pre-dorsal distance 65·2, pre-anal distance 54·3, length of anal base 48·5.

Dorsal iv 12, pectoral i 13, anal iii 54. Abdominal scutes 29. Branchiostegal rays 6. Gillrakers, 25 on lower part of first arch.

Maxilla rounded posteriorly, projecting beyond posterior tip of second supramaxilla. Dorsal origin well behind anal origin ; pelvic fins entirely absent.

COLOUR : " Uniform pale brown. Dusky brown median streak down back. Top of head and ends of jaws sprinkled with dusky dots. Iris and side of head silvery white. Fins pale. Pectoral and caudal with few dull dusky dots." (Fowler 1956).

SIZE : 136 mm. (208 mm. Fowler 1941).

RANGE : Gulf of Oman (Oman, Jask), but not from Persian Gulf, Red Sea or Gulf of Aden ; elsewhere, India, China, East Indies.

Specimens :

1 fish, 136 mm., off Jask, coll. Blegvad (Z.M.C. —C 1).

ILISHA Richardson, 1846

Ilisha (Gray) Richardson, 1846, *Ichth. China Japan* : 306 (Type : *Ilisha abnormis* (Gray) Richardson).

Platygaster Swainson, 1839, *Nat. Hist. Animals*, **2** : 294 (Type : *Clupea africana* Bloch) (*non Platygaster* Latreille 1809, Schilling 1829, Duméril and Bibron 1844).

Zunasia Jordan and Metz, 1913, *Mem. Carnegie Mus.*, **6** (1) : 7 (Type : *Pristigaster chinensis* Basilewsky).

Euplatygaster Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 (Type : *Pellona brachysoma* Bleeker).

A single species recorded from this area.

Ilisha indica (Swainson)

Platygaster indicus Swainson, 1839, *Nat. Hist. Animals*, **2** : 294 (on *Ditchoee* Russell, 1803, *Fishes of Coromandel*, **2** : 74, pl. 192 [upper figure] ; Type locality : Vizagapatam).

Ilisha indica : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 67, fig. 30 (photo) (off Bushire, W. of Kharg, Bushire Roads).

? *Ilisha filigera* : Misra, 1947, *Rec. Indian Mus.*, **45** : 116 (Persian Gulf).

Misra's specimen of *I. filigera* may have been this species, but no description is given. Fowler (1941) places *I. filigera* in the second part of his key, i.e. those species with more than 46 scales and 20–28 pre-pelvic scutes. Scales are missing from the Blegvad specimens, but there are 20–22 pre-pelvic scutes. However, the Blegvad fishes are clearly distinct from the species included by Fowler in the second half of his key on a combination of characters (gillraker number, anal position, scute number, anal finray number), and in all these features they agree with *I. indica*. The genus *Ilisha* is badly in need of revision.

DESCRIPTION : based on three fishes, 155–188 mm., from the Persian Gulf.

In percentages of standard length : body depth 33·0–34·0, head length 25·4–26·5 ; snout length 6·5–7·4, eye diameter 7·8–8·6, upper jaw length 12·3–12·7, lower jaw length 12·1–13·0 ; pectoral length 17·4–17·9, pelvic length 5·1–5·3, anal base 30·5–32·2 ; pre-dorsal distance 47·7–49·5, pre-pelvic length 47·3–47·5, pre-anal length 66·0–68·0.

Dorsal iii 15–16, pectoral i 15–16, pelvic i 6, anal iii 39–40. Abdominal scutes, 20–22 pre-pelvic, 10 post-pelvic, total 30–32. Gillrakers on lower part of first arch 25–26.

COLOUR : in alcohol, a uniform pale brown, slightly darker along back, fins hyaline.

SIZE : 188 mm. (" up to 40 cm. " Blegvad 1944).

RANGE : Persian Gulf only (Bushehr, Kharg) ; elsewhere, East Africa, India, East Indies, China.

Specimens :

8 fishes, 61.5–72·5 and 155–188 mm., Persian Gulf, coll. Blegvad (Z.M.C. C 1–8).

Subfamily DOROSOMATINAE (Gizzard shads)

Five Indo-Pacific genera, two recorded from the Red Sea area, but not from the Red Sea itself. Genera reviewed by Whitehead (1962b).

KEY TO THE GENERA

1 Last dorsal ray produced as a filament . . . . ***Nematalosa***
2 Last dorsal ray not produced . . . . ***Anadontostoma***

NEMATALOSA Regan, 1917

Nematalosa Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 313 (Type : *Clupea nasus* Bloch, designated by Jordan, 1920, *Genera of Fishes*, pt. 4 : 560).

Two species found in this area.

KEY TO SPECIES

1 Snout not projecting greatly beyond tip of lower jaw ; maxilla not curved strongly downwards at tip ; second sub-orbital with oblique lower edge ; head longer, 29–32% of S.L. . . . . ***N. arabica***
2 Snout projecting well beyond tip of lower jaw, the mouth clearly inferior ; maxilla short, its tip curved strongly downwards ; second suborbital with vertical anterior edge ; head shorter, 25% of S.L. . . . . ***N. nasus***

Nematalosa arabica Regan

Nematalosa arabica Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 313 (Muscat : Boulenger's Muscat specimen of *C. nasus*) ; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 554 (compiled) ; *Idem*, 1956, *Fishes of the Red Sea* : 60 (copied) ; Tortonese, 1957, *Boll. Mus. Civ. Stor. nat. Venezia*, **10** : 123 (Ras Hafur) ; Whitehead, 1962, *Bull. Brit. Mus. nat. Hist.*, **9** (2) : 98, figs. 1B, 2B, 3A (Muscat, Mukalla, Jibuti).

Chatoessus nasus Boulenger, 1887, *Proc. zool. Soc. London* : 66 (Muscat).

DESCRIPTION : based on the holotype, 131 mm. standard length from Muscat ; one fish, 150 mm., from Mukalla ; and six fishes, 94–101 mm., from Jibuti.

In percentages of standard length : body depth 36·0–40·5, head length 29·3–31·7, head depth at occiput 23·4–26·0 ; snout length 6·1–7·6, eye diameter 7·3–7·8, post-orbital distance 13·9–15·3, pre-maxilla length 4·5–5·7, upper jaw length 6·5–8·2 ; pectoral length 20·5–23·0, pelvic length 12·4–14·0, length of anal base 15·3–17·9 ; pre-dorsal distance 49·0–51·0, pre-pelvic distance 52·0–54·5 ; length of last (filamentous) dorsal ray 35·5–41·0 ; depth of caudal peduncle (11·0) 12·1–12·9.

Pre-maxilla 1·14–1·77 times in length of maxilla ; length of expanded portion of maxilla 2·40–3·40 times in the length of the whole bone, the depth of the expanded portion 2·57–3·13 times in maxilla length. Maxilla reaching to below anterior pupil border.

Gillrakers about half length of gill filaments on anterior arch ; anterior hemibranch equal or subequal to posterior hemibranch.

Dorsal iv–v 12–14 (total 17–18), anal ii–iii 15–17 (total 18–20) ; scales in lateral series 42–45 ; abdominal scutes, pre-pelvic 18–19, post-pelvic 13–15, total 32–34 ; vertebrae 46 (1 specimen).

Pelvic fin base below second or third branched dorsal ray ; pectoral tips reach or almost reach pelvic base. Sub-operculum roughly rectangular ; anterior margin of second sub-orbital with oblique lower edge.

LENGTH : 150 mm.

RANGE : Gulf of Oman (Muscat), Gulf of Aden (Mukalla, Alayu, Ras Hafun and Djibuti), but no records from Red Sea itself or Persian Gulf. Not known outside this area.

Specimens :

1 fish, 131 mm., HOLOTYPE, Muscat (B.M.N.H. 1887.11.11.312).
1 fish, 150 mm., Mukalla (B.M.N.H. 1945.12.31.14).
6 fishes, 94–101 mm., Jibuti, Somaliland (B.M.N.H. 1962.3.13.1–6).
2 fishes, 51–52 mm., Alayu, Gulf of Aden (B.M.N.H. 1962.3.13.7–8).

Nematalosa nasus (Bloch)

Clupea nasus Bloch, 1795, *Naturgesch. Ausl. Fische*, **9** : 116, pl. 429, fig. 1 (Malabar).

Dorosoma nasus : Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 156 (Tamarida and Kor Garrieh, Gischin), 167 (S. and E. coasts Arabia) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 58, fig. 26 (copied Day) (Bushire Roads).

Nematalosa nasus : Misra, 1947, *Rec. Indian Mus.*, **45** : 116 (Hor-el-Hammar) ; Menon, 1960, *Rec. Indian Mus.*, **54** : 141 (Hor-el-Hammar) ; Mahdi, 1962, *Fishes of Iraq* : 13 (Hor-el-Hammar) ; Khalaf, 1962, *Mar. f-water fishes of Iraq* : 20 (Shatt-el-Arab, Hor-el-Hammar).

DESCRIPTION : based on two fishes, 97·5 and 152·0 mm., from Bushire, Persian Gulf (Blegvad's two specimens). Measurements for larger fish stated first.

In percentages of standard length : body depth 37·8 and 42·2, head length 24·8 and 25·2 ; snout length 6·3 and 6·4, eye diameter 5·5 and 7·2 ; pectoral length 24·2 and 24·0, pelvic length 12·9 and 12·9, last dorsal ray 40·7 and 37·3, pectoral axillary scale 10·9 and 5·1 ; pre-dorsal distance 47·0 and 51·5, pre-pelvic distance 51·0 and 52·0, pre-anal distance 76·0 and 76·5.

Gillrakers less than half length of gill filaments on anterior arch ; anterior hemibranch equal or subequal to posterior hemibranch.

Dorsal iv 11 and 12, pectoral i 14 and 15, anal ii 16 and 20. Abdominal scutes, pre-pelvic 18 and 20, post-pelvic 13 and 12, total 31 and 32.

Pelvic fin base under first or second branched dorsal ray. Pectoral tips just fail to reach pelvic base. Sub-operculum roughly rectangular ; anterior margin of second sub-orbital not clearly defined, but probably vertical, not with oblique lower edge. A recent description of the skull is given by Moona (1964).

LENGTH : 152 mm. (220 mm. Weber and de Beaufort 1913).

RANGE : Persian Gulf (Bushehr, Hor-el-Hammar), and Gulf of Aden (Tamarida, Kor Garrieh, Qishn), but no Red Sea records ; elsewhere, Indian Ocean, Malay Archipelago, ? Philippines and China.

Specimens :

2 fishes, 98–152 mm., Bushire (Blegvad material, Z.M.C. C4–5).
1 fish, 142 mm., Shatt-el-Arab, coll. Pietschmann (N.M.V. 4345).

ANODONTOSTOMA Bleeker, 1849

Anodontostoma Bleeker, 1849, *Verh. Bat. Gen.* (*Madura*), **22** : 15 (Type : *Anodontostoma hasselti* Bleeker = *Clupanodon chacunda* Hamilton-Buchanan).

A single species in this area.

Anodontostoma chacunda (Hamilton-Buchanan)

Goaf (Iran)

Clupanodon chacunda Hamilton-Buchanan, 1822, *Fishes of the Ganges* : 246, 283 (Type locality : Ganges estuaries).

Dorosoma chacunda : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 59 (S. of Ras el Mutafs between Lingeh and Quishim).

Anodontostoma chacunda : Fowler 1956, *Fishes of the Red Sea*, **1** : 60 (Indo-Pacific specimens only).

Description : based on two fishes, 118–128 mm., Persian Gulf.

In percentages of standard length : body depth 47·0–50·7, head length 26·0–27·4 ; snout length 5·6–6·1, eye diameter 8·2–8·4 ; pectoral length 23·7–24·5, pelvic length 14·3–14·8, anal base 17·9–19·1 ; pre-dorsal distance 50·5–50·8, pre-pelvic distance 54·0–57·5, pre-anal distance 79·0–82·0.

Dorsal iv 15, pectoral i 15–16, pelvic i 7, anal iii 16–17. Abdominal scutes, 17 pre-pelvic, 10–11 post-pelvic. Gillrakers, 64–65 on lower part of first arch. Scales in lateral series 40–44 (Fowler 1941).

Colour : in alcohol, light brown, darker along back, scale rows marked by paler horizontal lines ; a large black spot (almost equal to eye) a little behind operculum, on a level with eye ; fins hyaline.

Length : 128 mm. (212 mm., Fowler 1941).

Range : Persian Gulf (between Lingeh and Qeshm) ; elsewhere, Indian Ocean to East Indies, Philippines, Hainan, Melanesia.

Specimens :

2 fishes, 118–128 mm., Persian Gulf, col. Blegvad (Z.M.C. C10–11).

ENGRAULIDAE

Four genera found in the Red Sea area, *Engraulis*, *Stolephorus*, *Thrissina* and *Thryssa*, of which the first is represented only by immigrants from the Mediterranean.

KEY TO THE GENERA

1 No abdominal scutes, belly rounded and smooth . . . . . . ***Engraulis***
2 Abdominal scutes present :
  a. No post-pelvic scutes . . . . ***Stolephorus***
  b. Post-pelvic scutes present :
    i. No scutes before pectorals . . . . ***Thrissina***
    ii. Pre-pectoral scutes present . . . . ***Thryssa***

ENGRAULIS Cuvier, 1817

Engraulis Cuvier, 1817, *Règne Animal*, **2** : 174 (Type : *Clupea encrasicolus* Linnaeus, designated by Jordan, Tanaka and Snyder, 1913, *J. Coll. Sci. Tokyo*, **33** : 38).
Encrasicolus Fleming, 1828, *Hist. Brit. Anim.* : 183 (Type : *Clupea encrasicolus* Linnaeus).
Austranchovia Whitley, 1931, *Aust. Zool.*, **6** : 311 (Type : *Atherina australis* Shaw).

In addition to the well-known forms of *Engraulis* in temperate waters (Atlantic and Pacific coasts of North and South America, coastal waters of Japan, Australia, and South Africa, and in the Eastern Atlantic and Mediterranean region), I have shown elsewhere that a smaller, tropical form exists off the coasts of West Africa and in parts of the Indo-Pacific (Whitehead 1964c). Small specimens of *Engraulis* are readily mistaken for species of the closely related *Stolephorus*, and because of the reputedly strict antitropical distribution of *Engraulis* such confusion has been responsible for authors overlooking the occasional presence of *Engraulis* from tropical regions in their collections.

From the Red Sea region, however, the only specimens of *Engraulis* which I have found are those recorded by Norman (1927) from Port Said and the Great Bitter Lake. Bleeker's eleven syntypes of *Stolephorus zollingeri* are all *Engraulis* (Whitehead 1964b), but Blegvad's three specimens of *S. zollingeri* from the Persian Gulf are true *Stolephorus*.

Engraulis and *Stolephorus* can be separated by the presence, in the latter, of a pair of triangular fontanelles between the posterior tips of the frontals. These fontanelles, which are narrowly divided in the midline by the anterior extension of the supraoccipital, occur also in *Thrissina* and *Thryssa*, but not in adult *Engraulis*. A second difference between *Engraulis* and *Stolephorus* is in the length of the pseudobranch, which exceeds eye diameter in *Engraulis* but is shorter in *Stolephorus*. Finally, the maxilla in *Engraulis* barely projects beyond the posterior tip of the second (posterior) supra-maxilla ; in most species of *Stolephorus* it projects at least a short distance beyond.

Engraulis encrasicolus (Linnaeus)
(Antchonga)

Clupea encrasicolus Linnaeus, 1758, *Syst. Nat.* ed. 10, **1** : 318 (" Oceano Europaeo ").
Engraulis encrasicolus : Jordan and Hubbs, 1917, *Ann. Carnegie Mus.*, **11** (3–4) : 461 (Port Said) ; Chabanaud, 1932, *Bull. Mus. Hist. nat. Paris*, (2) **4** (7) : 824 (Lac Amer, Suez Canal) ; *Idem*, 1934, *Bull. Mus. Hist. nat. Paris*, (2) **6** (1) : 157 (L. Timsah, Suez Canal) ; Fowler, 1956, *Fishes of the Red Sea*, **1** : 72 (Italian specimens).
Engraulis encrasicholus : (misspelt) Norman, 1927, *Trans. zool. Soc. London*, **23** (3) : 376 (Port Said, Lake Manzaleh, Great Bitter Lake) ; Gruvel and Chabanaud, 1937, *Mém. Inst. Egypte*, **35** : 4 (Suez Canal).
Engraulis anchrassicolus : (error) Gruvel, 1936, *Mém. Inst. Egypte*, **29** : 151 (Suez Canal).

Description : based on the single specimen, 68 mm., recorded by Norman from the Great Bitter Lake ; and on two fishes, 75–93 mm., from Port Said. A good description, and comparisons between samples from different parts of the Mediterranean region, are given by Demir (in press).

In percentages of standard length : body depth 17·9–21·5, head length 26·4–29·2 ; snout length 4·8–5·2, eye diameter 6·5–7·8, maxilla length 20·4–23·2, length of lower jaw 18·5–19·6 ; pectoral length 14·7–17·7, pelvic length 10·2–13·8, length of anal base 14·7–17·5 ; pre-dorsal distance 51·5–54·5, pre-pelvic distance 46·0–51·4, pre-anal distance 68·0–71·0.

Dorsal iii 12, pectoral i 14–15, pelvic i 6, anal ii 15–16. No abdominal scutes, but a single pelvic scute with tapering ascending arms. Scales deciduous. Gillrakers 32–33 on lower part of first arch. Branchiostegal rays 12–13.

Colour : in alcohol, upper and lower surfaces brown, broad silvery stripe along flank (width exceeding eye diameter), belly silver to pelvic fin base. Fins hyaline.

Length : 93 mm. (Port Said) ; elsewhere up to 180 mm., Adriatic, Demir (in press).

Range : Suez Canal (Great Bitter Lake, but not beyond according to Norman (1927)—to Gulf of Suez according to Tillier (1902)) ; elsewhere, Mediterranean region (Black Sea, Sea of Azov, Mediterranean), Eastern Atlantic from Bergen to Morocco. Eggs (or larvae) from Gulf of Suez reported by Fage (1920) may have been based on a species of *Stolephorus*.

Specimens :

1 fish, 68 mm., Great Bitter Lake (B.M.N.H. 1925.12.31.1).
2 fishes, 75–93 mm., Port Said (B.M.N.H. 1925.9.19.6–7).

STOLEPHORUS Lacepède, 1803

Stolephorus Lacepède, 1803, *Hist. Nat. Poiss.*, **5** : 381 (Type : *Stolephorus commersonii* Lacepède —see Whitehead 1963c, Proposal Z.N. (S) 569, *Bull. zool. Nomencl.*, **20** (4) : 281–284).
Anchoviella : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 696 (*non* Fowler 1911).
Amentum Whitley, 1940, *Aust. Zool.*, **9** (4) : 402 (Type : *Stolephorus commersonii* Lacepède).

Note on synonymy.

Elsewhere (Whitehead 1963c) I have shown that the identity of *Atherina japonica* Houttuyn, the second of the two species included by Lacepède in his genus *Stolephorus*, cannot be deduced with certainty. Authors have sometimes considered it a species of round herring and accordingly have either used *Anchoviella* Fowler, an American genus, to take the place of *Stolephorus* for Indo-Pacific species (e.g. Fowler 1941) ; or have proposed a new name (e.g. Whitley 1940). As pointed out by Gosline (1951), the International Commission for Zoological Nomenclature had some years ago (Opinion 93, 1926) designated *Stolephorus commersonianus** Lacepède, an undoubted anchovy, the type of *Stolephorus*. *Atherina japonica* Houttuyn should be considered a *nomen dubium* (Whitehead 1963c).

The genus *Stolephorus* is badly in need of revision and, as in the case of *Sardinella* and *Herklotsichthys*, a full revision may well reduce the number of species at present recognised (e.g. Fowler 1941, 15 species, separated chiefly on scute number, maxilla length and anal position).

*A cheironym for *commersonii*.

KEY TO SPECIES

1 Anal origin under or behind last dorsal ray ; muscular portion of isthmus not reaching to border of branchiostegal membrane.
  a. maxilla pointed posteriorly, projecting beyond second supramaxilla **S. heterolobus**
  b. maxilla truncate posteriorly, barely projecting beyond second supramaxilla **S. buccaneeri**

2 Anal origin under dorsal ; muscular portion of isthmus reaching forward beyond hind border of branchiostegal membrane ; maxilla tip pointed, projecting beyond second supramaxilla . . . . **S. indicus**

Stolephorus heterolobus (Rüppell)
(Antchonga, Hanen)

Engraulis heteroloba Rüppell, 1837, *Neue Wirbelth., Fische* : 79, pl. 21, fig. 4 (Type locality : Bay of Massaua) ; Martens, 1866, *Verh. zool. bot. Ges. Wien*, **16** : 379 (Koseir).

Engraulis heterolobus : Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 392 (Red Sea) ; Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 596 (Koseir, Red Sea) ; Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 157 (Gischin), 167 (S. Arabia) ; Gruvel, 1936, *Mém. Inst. Egypte*, **29** : 151 (Suez Canal) ; Gruvel and Chabanaud, 1937, *loc. cit.*, **35** : 4 (idem) ; Bertin, 1943, *Bull. Mus. Hist. nat. Paris*, (2) **15** (6) : 389 (Gulf of Suez ; L. Timsah ; Djibouti).

Anchoviella heteroloba : Fowler, 1945, *Sudan Notes and Records*, **26** (1) : 116 (Red Sea).

Stolephorus heterolobus : Bertram, 1948, *Fish. Sultinate Muscat Oman* : 26 (Batinah coast).

Amentum heterolobum : Fowler, 1956, *Fishes of the Red Sea*, **1** : 73 (Buru and Philippine specimens only).

Engraulis commersonianus : Boulenger, 1887, *Proc. zool. Soc. London* : 666 (Muscat) (misidentification) ; ? Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 167 (E. Arabia) (name only ; ? on Boulenger).

DESCRIPTION : based on the holotype, 60·0 mm. standard length, from the Bay of Massawa ; five fishes, 53–55 mm. standard length, from Muscat (Boulenger's *E. commersonianus*) ; six fishes, 44–59 mm., from Ras Imran, Gulf of Aden ; and ten fishes, 59-64 mm., from Dulcuff I.

In percentages of standard length : body depth (15·0, holotype) 14·4–18·2, head length 24·5–29·0 ; snout length 4·7–6·3, eye diameter 6·4–7·7, upper jaw length (21·7, holotype) 21·3–25·9, lower jaw length 15·8–19·5 ; pectoral length 12·2–14·5, pelvic length 7·9–9·5, length of anal base 14·3–19·4 ; pre-dorsal distance 49·5–54·0 (55·5, holotype), pre-pelvic distance 43·6–50·5, pre-anal distance 62·5–67·7.

Anterior tip of muscular portion of isthmus lying well behind margin of branchiostegal membrane ; urohyal with a horizontal, shield-shaped expansion on lower edge immediately in front of the muscular portion of isthmus (Figure 4a). Maxilla tip pointed, reaching to just beyond lower jaw articulation. Anal origin below or behind last dorsal ray.

Dorsal iii 10–11, pectoral i 11–13, pelvic i 7, anal ii–iii 13–15 (15–18 total). Abdominal scutes, 5–6 pre-pelvic only. Scales caducous, 33–34 in lateral series (Fowler, 1956). Gillrakers, upper arch (23 in holotype) 17–20, lower arch 21–25 (26 in holotype).

COLOUR : in alcohol, dark brown upper surfaces, lighter brown lower surfaces, a broad silver lateral band on flanks, wider then eye diameter. Fins hyaline.

LENGTH : 60 mm. (73 mm. Fowler, 1956).

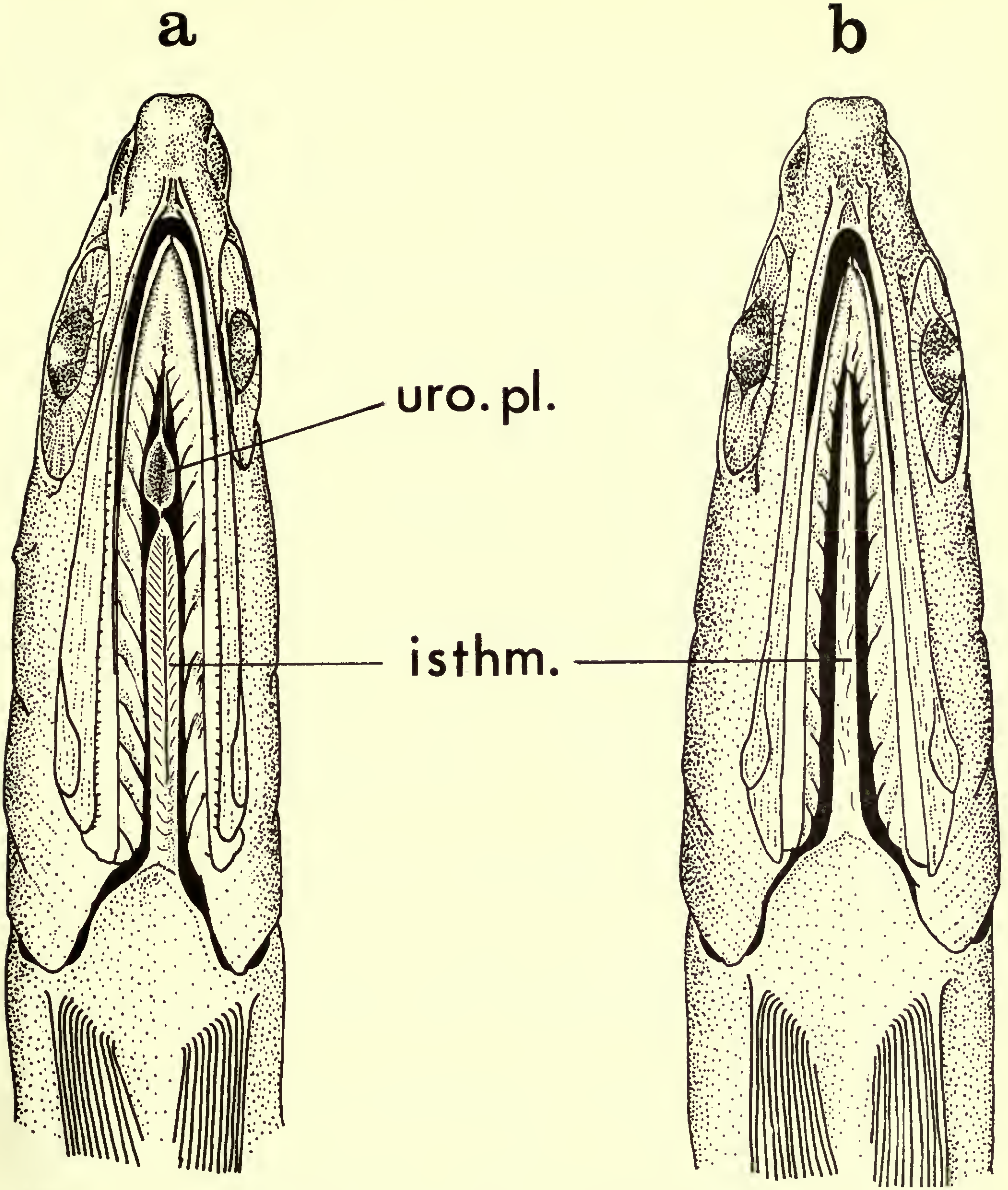

FIG. 4. Ventral view of head in two species of *Stolephorus* showing relative lengths of muscular portion of isthmus and position of ventral expansion on urohyal. a. *S. heterolobus*. b. *S. indicus*.

uro. pl.—urohyal plate. *isthm.*—muscular portion of isthmus.

RANGE : Suez Canal, Lake Timsah, Red Sea (Quseir, Abayil, Kamaran, Massawa, Dulcuff I.), Gulf of Aden (Ras Imran, Ras Antara, Berbera, Djibuti), Gulf of Oman (Muscat), Persian Gulf (Bendar Abbas) ; elsewhere, Zanzibar, Madras, East Indies, Australia.

Specimens :

1 fish, 60 mm., HOLOTYPE of *Engraulis heterolobus* Rüppell, Red Sea (B.M.N.H. 1845.10.29.104).

3 fishes, 62–64 mm., PARATYPES of *E. heterolobus* Rüppell, Massaua (N.-M.F.-I.S. 4715–17).

10 fishes, 53–55 mm., Muscat (Boulenger's *Engraulis commersonianus*) (B.M.N.H. (1887.11.11.302–311).

54 fishes, 33–39 mm., Ras Imran (B.M.N.H. 1963.12.9.36–55).

5 fishes, 51–61 mm., Berbera (B.M.N.H. 1963.12.9.56–59).

6 fishes, 27–29 mm., Ras Antara (B.M.N.H. 1963.12.9.31–35).

2 fishes, damaged, Bendar Abbas, Blegvad material (Z.M.C. 4–8).

13 fishes, 56–62 mm., Dulcuff I., Red Sea (H.U. E57/731).

5 fishes, 43–51 mm., " Arabia, ? Oman " (H.U. 2087/4–5).

2 fishes, 48 mm., Massaua (H.U. E57/769).

4 fishes, 49–58 mm., Cameran, Red Sea, coll. Steindachner (N.M.V. 2757).

1 fish, 51 mm., Abayil, Red Sea, coll. Steindachner (N.M.V. 2756).

NOTE ON MATERIAL EXAMINED : *S. heterolobus* belongs to the group of species in which the anal origin lies behind or below the last dorsal ray. This group includes *S. zollingeri* (Bleeker), *S. celebicus* Hardenberg, *S. pseudoheterolobus* Hardenberg, *S. purpureus* Fowler and *S. buccaneeri* Strasbourg. I have shown elsewhere (Whitehead 1964b) that *S. zollingeri* (and possibly also *S. celebicus*) was based on specimens of *Engraulis*. *S. pseudoheterolobus* was distinguished by Hardenberg (1933) from *S. heterolobus* by its longer maxillary (21·3–22·7 per cent of S.L.) and deeper body (16·1–17·9 per cent of S.L.) ; these figures are, however, almost identical with those given here for *S. heterolobus*. The two remaining species were described from Hawaii.

S. heterolobus differs from all other species in having a small plate-like bony expansion on the lower edge of the urohyal immediately in front of the muscular portion of the isthmus (see Figure 4a). In *S. purpureus* and *S. buccaneeri* there is a similar expansion but it is fleshy and smaller than in *S. heterolobus*. In these three species the muscular, pigmented portion of the isthmus does not extend forward to the hind border of the branchiostegal membrane, as is the case in all other species of *Stolephorus*.

If these two characters, anal position and urohyal shape, have real systematic value, then *S. heterolobus* is most closely allied to species from Hawaii. It is, therefore, of great interest that the following species, *S. buccaneeri*, hitherto known only from Hawaii, should now be recorded from the Red Sea area.

Stolephorus buccaneeri Strasburg

Stolephorus buccaneeri Strasburg, 1960, *Pacific Science*, **14** (4) : 396 (Type locality : Hawaii).

Stolephorus zollingeri (Blkr.) ? : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 61 (Bender Abbas market).

Amentum zollingeri : Fowler, 1956, *Fishes of the Red Sea*, **1** : 73 (on Blegvad).

Amentum commersonii : Fowler & Steinitz, 1956, *Bull. Res. Counc. Israel*, **5** B : 262 (Arabia, Oman?).

Note on synomy.

Blegvad's three hard and shrivelled specimens from the Bender Abbas market closely resemble *S. zollingeri* Bleeker. I would have followed Blegvad's indentification were it not that Bleeker's specimens are in fact a species of *Engraulis* (Whitehead 1964b). The only species of *Stolephorus* with such short, truncated maxillae are *S. buccaneeri* from Hawaii and *S. celebicus* Hardenberg from Java. The types of the latter are lost, but at least one specimen identified as *S. celebicus* from Java in the Leiden Museum is a species of *Engraulis*. The paratypes ot *S. buccaneeri*, however, are true *Stolephorus*, having posterior frontal fontanelles retained in the adults (see Whitehead 1964b).

A single specimen collected by Steinitz from ' Arabia ', and two fishes from Suez collected by Steindachner are also placed in *S. buccaneeri*. All these specimens resemble *S. buccaneeri* in having a short muscular portion of the isthmus, not reaching the hind border of the branchiostegal membrane, and a small fleshy expansion on either side of the lower edge of the urohyal, just in front of the muscular part of the isthmus (a precursor of the *S. heterolobus* condition?). I have examined one further specimen of *S. buccaneeri*, a fish of 72 mm. from Durban.

Meristic counts for the Red Sea and Persian Gulf specimens fall within the ranges given by Strasburg (1960) for Hawaiian specimens of *S. buccaneeri*. In proportional measurements they agree or differ only very slightly except in maxilla length, which is a little greater (16·2–19·8 per cent. of S.L. ; *cf.* 14·1–16·8).

The Red Sea and Persian Gulf specimens cannot be separated from Hawaiian specimens at subspecific level on meristic or proportional measurements. Since the number of specimens collected from either area is small, it is possible that *S. buccaneeri* occurs in intermediate areas but has been missed. *S. celebicus* might be this species, but it was described as lacking scutes (a further reason for believing it to have been based on a species of *Engraulis*). Fowler's (1941) specimens of *S. zollingeri* from the Philippines may be this species ; he describes 4–5 abdominal scutes.

DESCRIPTION : based on three specimens 40–50 mm. standard length, from Bendar Abbas ; one fish, 51 mm., from "Arabia" ; and two fishes, 72–79 mm., from Suez.

In percentages of standard length : body depth 15·2–17·7, head length 23·4–26·8 ; snout length 4·3–5·0, eye diameter 6·8–8·1, upper jaw length 16·2–19·8, lower jaw length 15·4–19·1 ; pectoral length 14·2–15·4, pelvic length 7·6–9·2, length of anal base 14·5–16·6 ; pre-dorsal distance 50·4–53·2, pre-pelvic distance 45·4–47·5, pre-anal distance 64·5–68·0.

Anterior tip of muscular portion of isthmus lying well behind margin of branchiostegal membrane. Urohyal with two fleshy flanges on either side of the lower edge just in front of muscular part of the isthmus. Maxilla tip truncate, barely projecting beyond tip of 2nd supra-maxilla, not reaching anterior border of pre-operculum. Anal origin just behind last dorsal ray.

Dorsal iii 12, pectoral i 14–15, anal ii 13–14, pelvic i 7. Abdominal scutes, 4–5 pre-pelvic only. Scales caducous, no count possible. Gillrakers long, slender, 19–24 + 22–34 (higher counts in larger fishes).

Colour : in alcohol, light brown with prominent silver lateral stripe, not as wide as eye diameter. Dark horizontal line at bases of upper caudal rays.

Size : 79 mm. (Suez) ; 51·5 mm. (Hawaii, Strasburg 1960), 72 mm., Durban.

Range : Red Sea (Suez), Persian Gulf (near Bendar Abbas), " Arabia " ; elsewhere, Western Indian Ocean (Durban), Hawaii (Oahu, Niihau).

Specimens :

2 fishes, 72–79 mm., Suez, Red Sea, coll. Steindachner (N.M.V. 2737).
1 fish, 51 mm., " Arabia ", coll. Steinitz (H.U. 2087 [a]).
3 fishes, 40–50 mm., Bender Abbas Market, coll. Blegvad (Z.M.C. 1–3).

Stolephorus indicus (van Hasselt)

Engraulis indicus van Hasselt, 1823, *Alg. Konst-en Letter-Bode*, **1** (No. 23) : 329 (Java).
Stolephorus indicus : Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 62, fig. 27 (copied Day) (near Henjam).
Amentum indicum : Fowler, 1956, *Fishes of the Red Sea*, **1** : 74 (Indo-Pacific specimens only).

Description : based on one fish, 103 mm. standard length, from the Persian Gulf ; three fishes, 76–116 mm., from the Gulf of Aqaba ; four fishes 87–103 mm., from North Massawa Channel ; and one fish, 99 mm., from Eritrea.

In percentages of standard length : body depth 16·9–18·7, head length 22·4–24·7 ; snout length 4·5–5·5, eye diameter 5·8–7·3, upper jaw length 18·2–20·0, projection of maxilla beyond 2nd supra-maxilla 1·7–2·3, lower jaw length 15·2–16·7 ; pectoral length 12·2–13·8, pelvic length 7·6–9·5, length of anal base 15·0–16·1 (18·1) ; pre-dorsal distance 52·4–55·5, pre-pelvic distance 42·2–44·3 (46·2), pre-anal distance (58·0) 60·2–64·0.

Anterior tip of muscular portion of isthmus reaching forward beyond hind border of branchiostegal membrane ; urohyal a simple vertical plate without horizontal flanges on lower edge in front of muscular portion of isthmus (Figure 4b). Maxilla tip pointed, reaching to just beyond anterior border of pre-maxilla. Anal origin below sixth branched dorsal ray.

Dorsal iii–iv 12–13, pectoral i (12) 13–14, pelvic i 7, anal iii 16–18. Abdominal scutes, 4–5 pre-pelvic only. Scales caducous, 35–37 in lateral series (Fowler 1956). Gillrakers long, slender 16–18 + 23–26. Branchiostegal rays 13 (5 fishes).

Colour : in alcohol, dorsal surfaces brown, ventral surfaces light brown, sometimes white. A silvery midlateral stripe, not as well-defined as in *S. heterolobus*, sometimes very faint. Fins hyaline.

Size : 116 mm. (Gulf of Aqaba) ; " 6 inches " (Fowler, 1956).

Range : Red Sea (Horgigo Bay, North Massawa Channel, Mocha, Hanfelu Bay), Persian Gulf (near Henjam), but not recorded from Suez Canal, or the Gulfs of Aden or Oman ; elsewhere, Indo-Pacific from Zanzibar to Formosa, Riu Kiu, Melanesia, Micronesia, Polynesia.

Specimens :

1 fish, 103 mm., near Henjam, Blegvad material (Z.M.C. No. 2).
3 fishes, 76–116 mm., Horgigo Bay (H.U. E61/19).

4 fishes, 87–103 mm., N. Massawa Channel (H.U. E57/730, 1–4).
1 fish, 99 mm., Eritrea (H.U. E57/697).
2 fishes, 35–65 mm., Mokha, Red Sea (N.M.V. 2755).
2 fishes, 69–70 mm., Hanfelu Bay (N.M.V. 2740).

THRISSINA Jordan and Seale, 1925

Thrissina Jordan and Seale, 1925, *Copeia*, No. 141: 30 (Type: *Clupea baelama* Forskål).

T. baelama, the only member of *Thrissina*, differs from species of *Thryssa* (i.e. *Thrissocles auct.*) in lacking scutes in front of the pectoral fins, in possessing a well developed pseudobranch, and in having a free spine in front of the dorsal fin so poorly developed that it is barely apparent. *T. baelama* is nearer to species of *Stolephorus* in its slender body, well-developed pseudobranch and fewer anal rays (27–30 ; cf. 32–47 in species of *Thryssa*), but it differs in possessing post-pelvic scutes. Thus *Thrissina* stands intermediate between *Stolephorus* and *Thryssa*.

Thrissina baelama (Forskål)

(Laaf, Baelama, Rambu, Sardin)

Clupea baelama Forskål, 1775, *Descript. Animal.*: 72 (Type locality : Djidda).

Engraulis baelama : Valenciennes, 1848, *Hist. Nat. Poiss.*, **21** : (26) 35 (Red Sea).

Engraulis boelama : Günther, 1866, *Fishes of Zanzibar* : 123 (Red Sea) ; *Idem*, 1868, *Cat. Fish. Brit. Mus.*, **7** : 393 (" Cosseir ") ; Klunzinger, 1871, *Verh. zool. bot. Ges. Wien*, **21** : 597 (Koseir, Red Sea) ; Günther, 1871, *Proc. zool. Soc. London* : 671 (Red Sea) ; Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 157 (Sheikh Othman), 167 (S. Arabia); Bamber, 1915, *J. Linn. Soc. London*, **31** : 478 (Sudanese Red Sea).

Thrissocles boelama : Tortonese, 1936, *Boll. Mus. Zool. Anat. comp. Univ. Torino*, ser. 3, **45** (63) : 14 (Massaua).

Thrissocles boelana (error) : Fowler, 1945, *Sudan Notes and Records*, **25** (1) : 116 (Red Sea).

Thrissocles baelama : Fowler, 1945, *Sudan Notes and Records*, **25** (1) : fig. 2 ; *Idem*, 1956, *Fishes of the Red Sea*, **1** : 72 (Indo-Pacific specimens) ; Fowler & Steinitz, 1956, *Bull. Res. Counc. Israel*, **5** B : 262 (Oman).

Description : based on ten fishes, 87–105 mm. standard length, from Jibuti and Mukalla; four fishes, 72–98 mm., from the Red Sea ; two fishes, 88–97 mm., from Bandar Kassim (Gulf of Aden) ; and four fishes, 61–76 mm., from Port Sudan.

In percentages of standard length : body depth 21·8–27·3 ; head length 25·8–29·3 ; snout length 4·1–5·7, eye diameter 5·7–7·0, upper jaw length 22·7–26·6, extension of maxilla beyond 2nd supra-maxilla 1·9–2·5, lower jaw length 18·8–22·4 ; pectoral length 15·4–19·1, pelvic length (12·6) 13·1–14·6, length of anal base (23·8) 24·7–28·7 ; pre-dorsal distance 48·0–52·3, pre-pelvic distance 43·0–47·7, pre-anal distance 62·7–70·3.

Pseudobranch well-developed, slightly longer than eye diameter. Maxilla tip pointed, reaching just beyond lower jaw articulation. Anal origin behind last dorsal ray.

Dorsal iii 11–13, pectoral i 12 (13), pelvic i 7, anal iii 27–30. Abdominal scutes, pre-pelvic 6 (7–8), post-pelvic 8–9 (10), total 14–16, absent in front of pectoral fins. Scales caducous, 37–38 in lateral series (Fowler 1956). Gillrakers moderately long and slender, 16–18 (19) + 20–23. Branchiostegal rays 12–13 (14).

Colour : in alcohol, dorsal surfaces dark brown, flanks and lower part of body light brown or silvery. No silver stripe on flanks. Fins hyaline.

Size : 105 mm. (Gulf of Aden) ; 131 mm. (Fowler, 1956).

Range : Red Sea (Jiddah, Quseir, Massawa, Marsa Haleib, Rabigh, Yanbu, Nr. Port Sudan), Gulf of Aden (Bandar Kassim, Djibouti, Mukalla, Sheikh Othman), apparently not recorded from Persian Gulf or Gulf of Oman ; elsewhere, Indo-Pacific region from Zanzibar to Philippines, Melanesia, Micronesia and Polynesia.

Specimens :

19 fishes, 76–105 mm., Jibouti and Mukalla (B.M.N.H. 1963.12.9.1–19).
2 fishes, 86–98 mm., Red Sea, coll. Botta (M.N.H.N. Paris, No. 198).
2 fishes, 88–97 mm., Bandar Kassim (B.M.N.H. 1963.12.9.20–21).
5 fishes, 69–73 mm., Cosseir, pres. Dr. Peters (B.M.N.H. 1865.6.12.4–8).
2 fishes, 72–76 mm., " Red Sea ? " (B.M.N.H. 1882.8.16.54–55).
4 fishes, 61–72 mm., near Port Sudan (B.M.N.H. 1963.12.9.27–30).
2 fishes, 83–93 mm., Rabegh, Red Sea, coll. Steindachner (N.M.V. 1989).
2 fishes, 90–97 mm., Jambo, Red Sea, coll. Steindachner (N.M.V. 1987).
2 fishes, 71–78 mm., Mersa Haleib, Red Sea, coll. Steindachner (N.M.V. 1985).

THRYSSA Cuvier, 1829

Thrissa : *non* Rafinesque, 1815 : Cuvier, 1817, *Règne Animal*, **2** : 176 (Type : *Clupea setirostris* Broussonet, designated by Jordan and Evermann, 1917, *Genera of Fishes*, pt. 1 : 98).

Thryssa Cuvier, 1829, *Règne Animal*, ed. 2, **2** : 323 (Type : *Clupea setirostris* Broussonet).

Thryssus Swainson, 1838, *Nat. Hist. Animals*, **1** : 279 (280) (Type : *Clupea setirostris* Broussonet).

Trichosoma : *non* Rudolphi, 1819 : Swainson, 1839, *Nat. Hist. Animals*, **2** : 292 (Type : *Thrissa hamiltoni* Gray).

Thrissocles Jordan and Evermann, 1917, *Genera of Fishes*, pt. 1 : 98 (Type : *Clupea setirostris* Broussonet).

Scutengraulis Jordan and Seale, 1925, *Copeia*, No. 141 : 30 (Type : *Clupea hamiltoni* Gray).

Note on synonymy.

Thrissa Cuvier 1817 is undoubtedly the correct original spelling, as defined in the International Code for Zoological Nomenclature 1961 (Art. 32 [a]). This being so, *Thryssa* Cuvier, 1829, is an unjustified emendation (Art. 33 [a] [ii]) and becomes an objective junior synonym of *Thrissa* Cuvier, 1817. Unfortunately, the latter was already occupied by *Thrissa* Rafinesque, 1815 (now a junior synonym of *Clupanodon* Lacepède, 1803). *Thryssa* Cuvier, 1829, is therefore, the next available name in the synonymy, and although differing from *Thrissa* by only one letter is not (Art. 56 [a]) a homonym of *Thrissa*. *Thrissocles* Jordan and Evermann cannot, therefore, replace *Thryssa*. The name *Thrissocles* has been widely used until now, but Barnard (1925) used *Thryssa*.

Key to the species of Thryssa

1 Spines on gillrakers of first arch of even length along raker ; gillrakers on lower part of first arch 12–17.
  a. Maxilla not reaching pectoral base ; anal rays 38–43 . . . ***T. hamiltonii***
  b. Maxilla extending to or just beyond pectoral base ; anal rays 43–49 . ***T. purava***
  c. Maxilla extending to beyond pelvic base ; anal rays 34–37 . . ***T. setirostris***
2 Spines on gillrakers of first arch with regular clumps of longer spines ; gillrakers on lower part of first arch 20–23 ; maxilla extending to pectoral base . ***T. vitrirostris***

Thryssa hamiltonii (Gray)

Thrissa hamiltonii Gray, 1832–4, *Illustr. Indian Zool. Hardwicke*, **2** : pl. 92, fig. 3 (no locality).

Engraulis vitrirostris : (part) Blegvad, 1944, *Danish Sci. Invest. Iran*, No. 3 : 60 (specimen No. 3 only—Bushire Harbour).

? *Thrissocles malabaricus* : Menon, 1960, *Rec. Indian Mus.*, **54** : 141 (Persian Gulf).

Note on synonymy

Blegvad's specimen No. 3, recorded as *Engraulis vitrirostris*, is now labelled C4. Although not entirely accurate, Blegvad's anal ray, scute and gillraker counts for No. 3, are closer to those of specimen C4 than to those of specimen C3. Blegvad (p. 61) felt that his No. 3 " might be determined as *E. grayi* Blkr. " (a synonym of *T. hamiltonii*). Both first gill arches are now missing, but Blegvad records 13 rakers (8–10 + 12–14 in *E. hamiltonii*). The short maxilla and high anal count clearly separate this fish from *T. vitrirostris*. There seems little doubt that specimens Nos. 3 and 4 have been wrongly labelled. Menon's record of *T. malabaricus* may have been this species ; no description was given.

Description: based on a single specimen, 97 mm. standard length, from Bushire Roads.

In percentages of standard length : body depth 27·7, head length 23·7 ; snout length 3·7, eye diameter 6·2, upper jaw length 24·0, projection of maxilla beyond 2nd supra-maxilla 6·9, lower jaw length 17·7 ; pectoral length 19·6, pelvic length 8·4, length of anal base 34·8 ; pre-dorsal distance 53·0, pre-pelvic distance 41·0, pre-anal distance 62·0.

Line of jaws when mouth closed set at an angle of about 30° to the horizontal. Maxilla tip not reaching base of pectoral fin. Pseudobranch not visible externally. Anal origin just behind last dorsal ray.

Dorsal with small free spine in front, iii 11, pectoral i 11, pelvic i 7, anal iii 39. Abdominal scutes, pre-pelvic 17, post-pelvic 11. Scales caducous, 43–45 in lateral series (Fowler 1941). Gillrakers, both first arches missing (13 on lower arch—Blegvad 1944), gillraker spines not with clumps of longer spines. Vertebrae 45 (X-ray count).

Colour : in alcohol, uniform pale brown, fins hyaline. Humeral venules with a few scattered melanophores.

Length : 97 mm. (225 mm. Fowler 1941).

Range : Persian Gulf only (Bushehr Harbour) ; elsewhere, Indo-Pacific region from India to Korea and to Queensland.

Specimens :

1 fish, 97 mm., Bushire Harbour, Blegvad's *Engraulis vitrirostris* No. 3 (Z.M.C. No. 4).

Thryssa purava (Hamilton-Buchanan)

Clupea purava Hamilton-Buchanan, 1822, *Fishes of the Ganges* : 238, 382 (Type locality : Ganges estuaries).

Thrissocles purava : Misra, 1947, *Rec. Indian Mus.*, **45** : 117 (Hor-el-Hammar).

Engraulis vitrirostris : (part), Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 60 (specimen No. 4 only : Bushire Roads).

Note on synonymy.

As discussed above, Blegvad's specimens Nos. 3 and 4 have been wrongly labelled. Blegvad (p. 61) considered the possibility that his other specimens might be *T. purava*, but felt that gillraker and anal ray counts did not support this. In Blegvad's specimen No. 4 (i.e. specimen now labelled C3, the largest fish in this batch), the low number of gillrakers (10 + 19) and the high anal count place this fish in *T. purava*.

Description : based on a single fish, 158 mm. standard length, from Bushire Roads.

In percentages of standard length : body depth 25·2, head length 22·8 ; snout length 3·8, eye diameter 4·7, upper jaw length 23·5, projection of maxilla beyond 2nd supra-maxilla 7·0, lower jaw length 17·0 ; pectoral length 19·2, pelvic length 8·7, length of anal base 36·0 ; pre-dorsal distance 51·5, pre-pelvic distance 41·0, pre-anal distance 62·0.

Line of jaws when mouth closed set at an angle of about 45° to the horizontal. Maxilla tip reaches pectoral base. Pseudobranch not visible superficially. Anal origin under last dorsal ray.

Dorsal with small free spine in front, iii 10, pectoral i 11, pelvic i 7, anal iii 41. Abdominal scutes, pre-pelvic 15, post-pelvic 10. Scales caducous, 35–40 in lateral series (Fowler 1941). Gillrakers short with spines becoming larger at tips, 10 + 19 ; vertebrae 46 (X-ray count).

Colour : in alcohol, uniform light brown with paler midlateral stripe. Fins hyaline. Humeral venules with a few scattered melanophores.

Length : 158 mm. (Persian Gulf).

Range : Persian Gulf only (Bushehr) ; elsewhere, India, East Indies, Bonin Islands, Melanesia (Fowler 1941).

Specimens :

1 fish, 158 mm., Bushire Roads, Blegvad's *Engraulis vitrirostris* No. 4, largest specimen (Z.M.C. C3).

Thryssa vitrirostris (Gilchrist and Thompson)

Lacheh, Kowa (at Bendar Abbas)

Engraulis vitrirostris Gilchrist and Thompson, 1908–11, *Ann. S. Afr. Mus.*, **6** : 201 (Localities : Natal ; inner Harbour, Durban) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 60 (all but specimens No. 3 and 4 ; S. of Bushire, Hor Musa, near Hormuz, Jabrin).

Thrissocles vitirostris : (misspelt) : Fowler, 1956, *Fishes of the Red Sea*, **1** : 71 (on Blegvad).

Description : based on 12 fishes, 65·5–132 mm. standard length, from the Persian Gulf and Gulf of Oman.

In percentages of standard length : body depth 24·0–28·6, head length 24·7–27·3 ; snout length 4·2–5·2, eye diameter 5·3–7·5, upper jaw length 28·0–30·6, projection of maxilla beyond 2nd supra-maxilla (7·8) 8·8–10·0, lower jaw length 18·5–20·4 (22·5) ; pectoral length 18·1–20·5, pelvic length 7·5–9·1 ; length of anal base (28·2) 31·3–33·8 ; pre-dorsal distance 50·5–53·2, pre-pelvic distance 43·5–46·2, pre-anal distance 61·5–65·5.

Line of jaws (when mouth closed) at an angle of about 30° to the horizontal. Maxilla tip reaches pectoral base. Pseudobranch not visible. Anal origin behind last dorsal ray.

Dorsal with small free spine in front, iii 10–11, pectoral i 11–12, pelvic i 7, anal iii 33 (1 fish), 34 (6), 35 (2), 36 (3). Abdominal scutes, 16–17 (19) pre-pelvic, 10–11 (12) post-pelvic, total 26–28 (31). Scales caducous, 44 in lateral series (Fowler, 1941). Gillrakers, 14–17 + 20–21 (23), moderately long and slender, gillraker spines arranged in clumps of longer spines interspersed by shorter spines. Branchiostegal rays 11–12. Vertebrae 43 (1 fish), 44 (8), 45 (3).

COLOUR : in alcohol, uniform, light brown, with lighter band along flank. Fins hyaline. Humeral venules with well-marked lines of melanophores. Gill arches bright orange in life in Indian specimens (Dutt 1961b).

SIZE : 132 mm. (Persian Gulf) ; 168 mm. (Fowler, 1941).

RANGE : Persian Gulf (Bushehr, Hor Musa, Jabrin, Hormuz), Gulf of Oman (Blegvad lists several station numbers sited along the northern shores from which specimens were taken but not kept), not from Gulf of Aden or Red Sea ; elsewhere, South Africa, India.

Specimens :

12 fishes, 66–132 mm., Persian Gulf, Blegvad material (Z.M.C. C1–2, 5–14).

NOTE ON MATERIAL EXAMINED : In meristic characters, these fishes fall well within the range given by Dutt (1961b) for Indian specimens.

Thryssa setirostris (Broussonet)

(Soti)

Clupea setirostris Broussonet, 1782, *Ichth.*, **1** : no pagination, pl. 2 (Type locality : Pacific near Tanna I., Society Group) ; *Idem*, 1788, *Tabl. Ichth.*: 186, pl. 76, fig. 218 (Red Sea).
Engraulis setirostris : Steindachner, 1907, *Denkschr. Akad. Wiss. Wien*, **71** (1) : 157 (Gischin).
Thrissocles setirostris : Fowler, 1956, *Fishes of the Red Sea*, **1** : 71 (Indo-Pacific specimens).

DESCRIPTION : based on ten fishes, 85–120 mm. standard length, from Mukalla and Jibuti ; and two fishes, 118–134 mm., from the Red Sea.

In percentages of standard length : body depth 25·0–27·6, head length 20·9–23·4 ; snout length 3·4–4·4, eye diameter 5·0–6·5, upper jaw length 51·5–58·0, lower jaw length 12·7–14·2 ; pectoral length (16·4) 18·3–22·2, pelvic length 11·6–13·3, length of anal base 29·5–36·0 ; pre-dorsal distance 50·8–55·0, pre-pelvic distance 40·7–44·1, pre-anal distance 56·0–63·2.

Maxilla tip reaching to beyond pelvic base. Lower jaw with ascending coronoid process, not found in other species of *Thryssa*.

Pseudobranch not visible. Anal origin just behind last dorsal ray.

Dorsal with small free spine in front, iii 11–12 (13), pectoral i 11–12, pelvic i 7, anal iii 31–34. Abdominal scutes, 16–18 pre-pelvic, 8–9 post-pelvic, total 24–27. Scales caducous, 40–42 in lateral series (Fowler, 1941). Gillrakers moderately long, blunt, 6 + 11–12. Branchiostegal rays 10.

Colour : in alcohol, uniform light brown, humeral venules with lines of melanophores. Fins hyaline.

Size : 134 mm. (Red Sea).

Range : Red Sea (no localities given), Gulf of Aden (Djibouti, Qishn, Mukalla), not recorded from Persian Gulf or Gulf of Oman ; elsewhere, Indo-Pacific region, from Natal to China, Queensland, Polynesia.

Specimens :

21 fishes, 68–120 mm., Mukalla and Jibuti (B.M.N.H. 1963.12.9.60–80).
20 fishes, 31–53 mm., Berbera, Gulf of Aden (B.M.N.H. 1963.12.9.81–90).
2 fishes, 118–134 mm., Red Sea, coll. Boré (M.N.H.N. 5887).

DISCUSSION

Both the Red Sea and the Persian Gulf are large, partially enclosed bodies of water with rather special hydrological conditions (chiefly high temperatures and high salinities). Both would be expected to contain a relatively large proportion of endemic species. In fact, Marshall (1950) found 15 out of the 114 species he collected from the Gulf of Aqaba to be either endemic to the Red Sea or distinguishable in minor ways from the species known in the Indian Ocean. Gohar (1954) estimated that some 15 per cent. of the 450 species recorded from the Red Sea were endemic, but pointed out that about 80 per cent. of Red Sea species have a wide distribution in the Indo-Pacific region. Amongst the species listed here, the degree of endemism is very low and the single endemic, *Nematalosa arabica*, is not recorded from the Red Sea itself, but from the Gulf of Aden. But, unlike the typical coral reef fishes, the elopoid and clupeoid species are in general wide-ranging, pelagic fishes not given to forming small isolated communities within which genetical isolation and divergence could occur. Thus, of the 31 species listed here (Table I), the overwhelming majority are known not only from the Indian Ocean, but range eastwards to the East Indies, the Philippines, in some cases to China, even to Hawaii. What contribution, therefore, can such a list make to the understanding of the faunal relationships of the Red Sea fishes ?

The first and most obvious feature of the list of species given in Table I is the absence of any Mediterranean species in the Red Sea. The only two Mediterranean clupeoids which have emigrated southwards through the Suez Canal are *Sardinella maderensis* and *Engraulis encrasicolus*, and no certain Red Sea record exists for either, even from the Gulf of Suez. More striking perhaps is the fact that, of the 17 elopoid and clupeoid genera listed here for the Red Sea area, only one (*Sardinella*) has a member in the Mediterranean fauna. It is worth noting, however, that of these 17 genera, only two others have populations in temperate waters, *Dussumieria* and *Etrumeus*, and it is these two alone which have managed to penetrate into the Eastern Mediterranean. One can conclude from this that, amongst the elopoid and clupeoid fishes, the Red Sea is now populated by tropical, mainly widespread Indo-Pacific species which are probably unlikely to establish populations in the Eastern Mediterranean. If, at any stage in its history, the Red Sea was colonised by Mediterranean clupeoid fishes, then these either failed to become established or were subsequently eradicated by geological events. The Mediterranean species *Sardinella aurita*, which has a wide distribution elsewhere in the world, is replaced by *S. longiceps* in the Indian Ocean, and even this species has not yet been recorded from the Red Sea.

In comparison with the Red Sea-Persian Gulf area, the Mediterranean region has no elopoids at all, and a poor clupeoid fauna (*Alosa, Sardina, Sprattus, Clupeonella, Sardinella*, and *Engraulis*). It is also poor in comparison with the Western North Atlantic (elopoids : *Elops, Megalops, Albula, Dixonina ;* clupeoids : *Etrumeus, Clupea, Sardinella, Harengula, Opisthonema, Alosa, Brevoortia, Odontognathus, Pristigaster, Ilisha, Rhinosardinia, Dorosoma, Neopisthopterus, Chirocentrodon, Jenkinsia, Engraulis, Anchoa, Anchovia, Anchoviella*). If, therefore, the Mediterranean was colonized by elopoid and clupeoid fishes from the Indian Ocean *via* the Red Sea, these have since died out. In fact the Mediterranean clupeoid fishes (except for the endemic *Clupeonella*) are identical, or closely related, to genera and species in the Eastern North Atlantic. Thus, whatever connections existed between the Red Sea (and Indian Ocean) and the Mediterranean in past geological times, the present elopoid and clupeoid fishes offer virtually no evidence in either area of this link nowadays.

Recent migration between these two areas *via* the Suez Canal has been mainly from the Red Sea to the Mediterranean rather than *vice versa*. Two Red Sea clupeoid species have reached the Mediterranean, *Dussumieria acuta* and *Etrumeus teres* ; as already stated, only two Mediterranean clupeoids have penetrated as far as Lake Timsah and the Bitter Lakes. It would seem that colonization of a relatively hyperthermal and hypersaline environment has been easier for Indian Ocean elopoids and clupeoids passing into the Red Sea, than for Mediterranean clupeoids.

A further point raised by the list of species given here is the curious appearance of *Stolephorus buccaneeri*, otherwise known only from Hawaii. Unfortunately, few critical comparisons exist of species or forms from the extreme east and west of the Indo-Pacific region. But such figures as are recorded for *Dussumieria acuta* (Whitehead 1963b) suggest a parallel with *S. buccaneeri*. Thus Bertin (1943a) commented on the similarity of *D. acuta* from the two ends of the Indo-Pacific, and described this phenomenon as " *evolution centrifuge* ", postulating that the ancestral forms had been forced outwards by developing, competitive forms. Populations of *S. buccaneeri* might, of course, exist in the intervening area, unrecorded or misidentified. There are no other species listed here with such a marked discontinuity in their distribution. *S. heterolobus* was not recorded by Fowler (1941) from India, but I have now examined a Madras specimen in this museum.

Speculation based on the absence of records is unsatisfactory, and a comparison between the species listed here from the Red Sea and those from the Persian Gulf would probably give an incorrect picture of colonization of the two areas. According to Table I, only seven species are common to both areas and, on the basis of the present, rather inadequate records, it appears that each area has nine or ten species not found in the other. Since many of these nineteen species are widespread in the Indo-Pacific region, their absence from one or other area must, for the time being, be considered due to inadequate collections. Two of the Red Sea species absent from the Persian Gulf (*Elops machnata* and *Sardinella jussieu*) have been recorded from the Gulf of Oman ; similarly, two of those Persian Gulf species (excluding *Hilsa* spp.) absent from the Red Sea have been recorded from the Gulf of Aden (*Sardinella bulan*, and *Nematalosa nasus*). Important in this connection are the seasonal variations in hydrological conditions and any thermal or other gradients which may occur in either area. Thus, some fishes enter the Red Sea from the Gulf of Aden only during the winter months, others penetrate only as far as the ' sill ' north of Bal-el-Mandab (the true oceanographic beginning of the Red Sea), and others again become increasingly rarer towards the northern end of the Red Sea (see Gohar 1954). Obviously, a mere list of recorded species will be misleading unless supported by hydrological data.

In conclusion, it can be said that the Western Indian Ocean is much poorer in both species and genera of clupeoid fishes than is the Eastern Indian Ocean and Indo-Malayan Archipelago. The Red Sea-Persian Gulf elopoids and clupeoids have been derived, therefore, from an already rather meagre faunal assemblage. Evidence that the Red Sea or the Persian Gulf should be considered as special units within the Indo-Pacific region is not provided by the elopoid or clupeoid fishes.

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It is a pleasure to acknowledge my gratitude to Dr. H. Steinitz, who not only made available all the Red Sea elopoid and clupeoid fishes in the Hebrew University, but helped me in many ways during my stay in Jerusalem and visit to Eilat. To Dr. Adam Ben-Tuvia go my sincere thanks for his assistance in collecting specimens and for lending material from the Sea Fisheries Research Institute, Haifa. Material was borrowed from a number of institutions, and I am especially grateful to the following for their help : Dr. M. Blanc, Museum National d'Histoire Naturelle, Paris (Valenciennes material) ; Dr. Paul Kähsbauer, Natural History Museum, Vienna (Steindachner material) ; Dr. Jørgen Nielsen, Zoological Museum, Copenhagen (Blegvad material) ; Dr. Fritz Rössell, Natur-Museum, Senkenberg (Rüppell material) ; Dr. L. P. Schultz, U.S. National Museum, Washington (paratypes of *S. buccaneeri*) ; Dr. Z Kozikowska, Museum Zoologiczne, Wroclaw, Poland.

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TABLE I

Records of elopoid and clupeoid species from the Red Sea and adjacent regions.

	Mediterranean Sea	Suez Canal	Red Sea	Gulf of Aden	Gulf of Oman	Persian Gulf
Elopidae						
Elops machnata			×	×	×	
Albulidae						
Albula vulpes			×	×		
Chirocentridae						
Chirocentrus dorab			×	×	×	×
Dussumieriidae						
Dussumieria acuta	×	×	×	×		×
Etrumeus teres	×		×			
Spratelloides gracilis		×	×			
Spratelloides delicatulus			×	×		
Clupeidae						
Herklotsichthys punctatus		×	×	×	×	×
Herklotsichthys vittatus			×	×		
Sardinella bulan				×	×	×
Sardinella longiceps				×	×	
Sardinella maderensis	×	×				
Sardinella jussieu		×	×	×	×	
Sardinella fimbriata			×			×
Sardinella sirm			×	×		
Hilsa kelee				×		×
Hilsa ilisha						×
Opisthopterus tadoore					×	
Ilisha indica						×
Nematalosa arabica				×	×	
Nematalosa nasus				×		×
Anodontostoma chacunda						×
Engraulidae						
Engraulis encrasicolus	×	×				
Stolephorus heterolobus		×	×	×	×	×
Stolephorus buccaneeri			×			×
Stolephorus indicus			×			×
Thrissina baelama			×	×		
Thryssa vitrirostris					×	×
Thryssa setirostris			×	×		
Thryssa hamiltoni						×
Thryssa purava						×
TOTAL 31	4	7	17	17	10	16

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ACANTHODRILIDAE AND EUDRILIDAE (OLIGOCHAETA) FROM GHANA

By R. W. SIMS

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SYNOPSIS

Fifteen species of Acanthodrilidae and Eudrilidae are reported in a collection of earthworms made in Ghana by Miss M. A. Tazelaar. Six are new, four being species of *Millsonia* and two are species of *Hyperiodrilus* ; keys are provided to all species of these genera.

INTRODUCTION

FEW oligochaetes have previously been reported from Ghana (Omodeo, 1958 : 100 *et seq.*) so it is not surprising that when new collections are examined they are found to contain a high percentage of hitherto undescribed forms (Clausen, 1963 and *in prep.:* Sims, 1964). While a member of the staff of University College Ghana, Miss Mary A. Tazelaar collected earthworms in several localities in Ghana, including Togoland, about half of the species have proved to be new. Among the material obtained, the families Acanthodrilidae* and Eudrilidae are best represented by a total of fifteen species which are reported here. Six are described for the first time, four being species of *Millsonia* Beddard, 1894, and two being species of *Hyperiodrilus* Beddard, 1891 *a*. In addition, one new species of *Libyodrilus* Beddard, 1891 *c*, will be described by Mrs. Clausen (1965) and three other Eudrilid species are listed which were described elsewhere and separated as a new genus, *Legonea*, (Clausen, 1963 ; Sims, 1964). The purpose of this report is to place on record details of the new material of the families Acanthodrilidae and Eudrilidae and, in particular, to describe the new species. Zoogeographical and other discussions are not attempted since it would appear to be premature at this stage to discuss the significance of the new species and records.

---

*Subfamily Octochaetinae.

I wish to express my gratitude to Miss Tazelaar for collecting these earthworms and for presenting them to the British Museum (Natural History). My thanks are also due to Dr. M. Dzwillo, Staatsinstitut und Zoologisches Museum, for his courtesy in giving me access to material in his charge when I visited Hamburg. Finally, I must thank Mrs. Martha Weis Clausen for her friendly co-operation when we found our investigations overlapping.

TAXONOMY

ACANTHODRILIDÆ (OCTOCHÆTINAE)

Benhamia esca (Stephenson, 1931)

Dichogaster esca Stephenson, 1931, Proc. zool. Soc. Lond., **1931** : 71 : Begoro, Akim, Ghana.

2 clitellate, 1 aclitellate specimen, Tafo, 17th October, 1952. 10 clitellate specimens, Tafo, 14th May, 1954. 1 clitellate specimen, Prempeh College, grounds, Kumasi, 17th November, 1955.

DESCRIPTION. *External Characters.* Length 150–233 mm., diameter 6–7 mm. Segments 206–272. Cuticle non-iridescent ; epidermis unpigmented, colour pale straw (specimens preserved in alcohol). First dorsal pore ?12/13, 13/14–18/19. Prostomium large, prolobous.

Setae ventral, closely paired. In the pre-clitellate region the setal areas are raised giving a triannulate appearance. Setal formula similar throughout body, $aa : ab : bc : cd = 4{\cdot}5 : 1 : 3 : 1$, $dd = \frac{3}{4}$ circumference (*ab* is slightly greater than *cd*, the difference being equal to about the diameter of one seta). Setae in the region of the spermathecal pores unspecialised. Penial setae present *xvii*, *xix* in setal ring, midway between *b* and *c*, other setae absent *xvii–xix*. Penial setae usually single, sometimes two or three present ; when multiple usually of differing lengths. Each penial seta is about 3 mm. long and proximally 0·1 mm. in diameter (Fig. 1a). The shaft is gently curved and tapers distally to a shoulder four-fifths along the length of the seta from where it becomes more tooth-like. Proximally to the shoulder the shaft is ornamented with numerous distally directed spines (Fig. 1b) ; the tooth-like, distal one-fifth is smooth.

Clitellum annular *xiv*, *xv–xx* (6 segments), extending dorsally to *xiii*, *xiv* and *xxi* (8 segments).

Genital field concave between setal lines *cc* on *xvii–xix* with small raised pads (Fig. 1c).

Male pores paired *xviii* midway between setal lines *b* and *c*. Each lies in a convex, outwardly curving seminal groove which passes between the penial setae in *xvii* and *xix*. Prostatic pores paired *xvii*, *xix* medially to setal line *c* and laterally to the penial setae at the ends of the seminal grooves, each pore is surrounded by a pair of tumid lips.

Female pores inconspicuous, paired *xiv* midway between setal lines *a* and *b*, $\frac{1}{2}$ *ab* anteriorly to the setal ring.

Spermathecal pores large, paired in furrows 7/8, 8/9 in setal line *b* ; with the ectal end of each spermathecal duct protruding as a small papilla. The area of the ventral surface bounded by the four spermathecal pores is swollen and the intersegmental furrows in this region deeper.

Genital papillae single, median ventral in furrows 10/11–14/15, glandular in appearance ; sometimes 16/17, 19/20 occasionally 18/19 when slightly pigmented ; paired 17/18. The posterior papillae are present only when the genital field is fully developed.

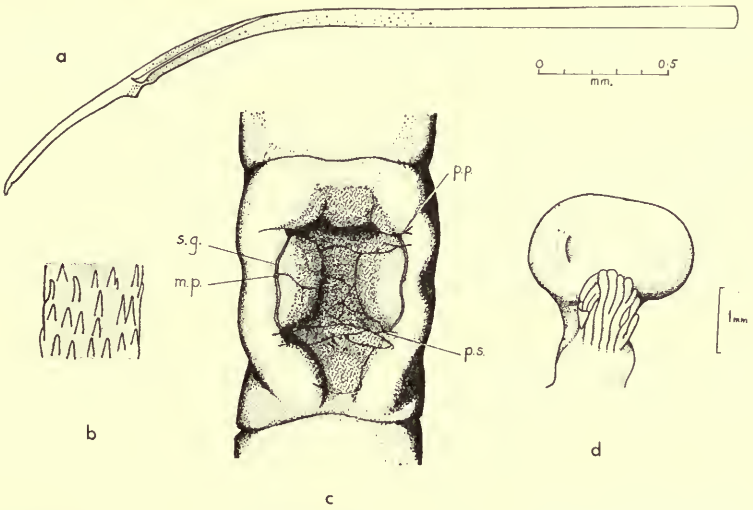

FIG. 1. *Benhamia esca* : a.—Penial seta (low power). b.—Penial seta (high power) showing spines, each spine is 30–50μ in length. c.—Genital field ; *m.p.*, male pore ; *p.p.*, prostatic pore ; *p.s.*, position of penial seta ; *s.g.*, seminal groove. d.—Right posterior spermatheca, dorsal view.

Internal Characters. First septum 4/5, 4/5–12/13 thickened, septa 4/5–6/7 being very thick. Septa 4/5–11/12 conical.

A large pharynx extends posteriorly to *iii*, in *iv* a dilated oesophagus leads from the postero-ventral surface of the pharynx to the first gizzard in *v*. Two gizzards, one in each of *v* and *vi*, are joined intersegmentally by a short, narrow portion of oesophagus. Both are heart-shaped, the anterior gizzard being slightly larger and more rounded ; in both there is an anterior " auricular " portion which is less strongly muscular than the larger, posterior " ventricular " portion. Gizzards considerably displaced posteriorly, gizzard in *vi* lies within the parietes of *xi*. Oesophageal glands paired *xiv*, *xv*, *xvi* ; those in *xiv* being the smallest and in *xvi* the largest. The glands of each side intercommunicate and are attached to the oesophagus by a paired duct in *xv*. (Each pair of glands is supplied with paired segmental blood vessels.) Intestine begins in *xx* and the typhlosole arises in *xxi* reaching full size in *xxiv* as a broadly triangular ridge along the dorsal surface of the lumen of the intestine.

The dorsal vessel extends anteriorly to *iii* where it passes into the pharynx, in *xiii–xv* it is apparently contractile being moniliform in appearance. Commissural vessels present *v–xiii* (in one specimen also *xiii* but slender and non-contractile) ; contractile as functional lateral hearts only in *x–xii*. The commissural vessels join the dorsal and ventral blood vessels. A supraoesophageal blood vessel can be traced between the posterior end of the hinder gizzard in *vi* and the anterior oesophageal gland in *xiv*, it is interconnected with the dorsal vessel by the commissural vessels in *vii–xii*. Suboesophageal and subneural blood vessels not seen. (The anterior blood vessels are difficult to trace due to the great displacement of the foregut and the thick anterior septa).

Testes holandric, funnels large, paired in *x*, *xi*. Seminal vesicles small, paired in *xi*, *xii*, granular in appearance. Vesa deferentia slender, almost transparent, those of each side lying closely together on the parietes level with the ectal regions of the prostatic ducts. They pass into small bilobed, muscular, ejaculatory pouches embedded in the parietes in *xviii*, each pouch is about 1 mm. in diameter and partly covered with parietal muscle strands. Prostates tubular, paired in *xvii*, *xix*, each is highly convoluted and nearly 20 mm. long when unravelled and 1 mm. in diameter. Ectally each prostate becomes slenderer and muscular before dilating slightly into a strongly muscular portion which passes into the parietes laterally to the large sac of a penial seta.

Ovaries and funnels small, paired *xiii*.

Spermathecae paired, lying in the coelom apparently between septa 5/6, 6/7, latero-ventrally to the posterior region of the pharynx (the displacement of the foregut confuses the situation of the anterior organs). Each spermatheca is approximately 3 mm. long and comprises a large ampulla and short slightly dilated adiverticulate duct (Fig. 1d).

Excretory system meronephridial.

REMARKS. This species has not been recorded since Stephenson described it on two specimens with imperfectly developed clitella and genital fields. The present series agrees largely with the types, particularly in the form of the penial setae but there are a few differences due, presumably, to age. Apart from two specimens which closely resemble the type specimens all others appear to be more fully developed. New information is given, therefore, of the genital field, spermathecae, spermathecal and female pores, in addition to other minor details.

Stephenson reported that the intestine began in *xvii* whereas in the new material it begins in *xx*. This discrepancy cannot be resolved from a detailed examination of the types since the specimens are partly contracted, the prostates are poorly developed and the structures in the prostatic region have been dissected. There is no doubt about the position of the anterior end of the intestine in the present series since, like in ripe individuals of other related species, segments *xvii–xix* are each almost equal in length to two or three intestinal segments and the posterior region of the oesophagus can clearly be seen passing through them.

Millsonia pumilia sp. nov.

5 clitellate specimens. Forest near Prempeh College, Kumasi. 21 March, 1956. Holotype, British Museum (Natural History) Register No. 1964.2.15 ; paratypes, British Museum (Natural History) Register No. 1964.2.16–19.

DIAGNOSIS. *External Characters.* Length 94–112 mm., diameter 3 mm.. Segments 193–242. Unpigmented. First dorsal pore ? 9/10, 10/11. Prolobous. Setae small, ventral, closely paired. Genital and penial setae absent. Clitellum *xiii–xix* (7 segments), saddle-shaped. Male pores paired *xviiii.* Female pores closely paired *xiv.* Spermathecal pores large, paired 7/8, 8/9 extending across setal lines *ab.* Genital papillae paired in setal line *b*, 13/14, 14/15, 15/16 (3 pairs).

Internal Characters. First septum 4/5, 4/5–10/11 thickened. Gizzards *v*, *vi.* Oesophageal glands paired *xv–xvii.* Intestine begins *xix*, intestinal caeca *xxvii–xxx* (4 pairs). Typhlosole ribbon-like, arising *xxvii.* Last lateral hearts *xii.* Holandric, testes paired in testes-sacs *x*, *xi.* Seminal vesicles paired *xi*, *xii.* Prostates paired *xvii*, *xix*, tubular, straight or simply looped. Ovaries paired *xiii.* Spermathecae paired *viii*, *ix*, posterior pair larger ; each with rounded ectal diverticulum and digitiform diverticulum $\frac{1}{3}$ distance from ectal end of duct, ampulla simple. Meronephridial.

DESCRIPTION. *External Characters.* Length 94–112 mm., diameter 3 mm. Segments 193–242. Cuticle with slight blue-green iridescence particularly in the pre-clitellar region. Epidermis unpigmented (white in alcohol preserved specimens), body contents seen through the body wall. First dorsal pore ?9/10, 10/11, pores sometimes occluded in the clitellar region. Prostomium prolobous. Segments between 8/9 and clitellar region biannulate usually with each annulus subdivided, segments triannulate in the post-clitellar region.

Setae small, ventrally situated ; sometimes absent *xvii–xix.* Setal formula at *x* *aa* : *ab* : *bc* : *cd*=6 : 1 : 4 : 1, $dd=\frac{5}{7}$ circumference ; at *xv* 6 : 2 : 5 : 1, $dd=\frac{5}{7}$ circumference ; at *c* 6 : 1 : 4 : 1, $dd=\frac{5}{7}$ circumference. Genital and penial setae absent.

Clitellum saddle-shaped *xiii–xix.* Genital field raised, well-developed $\frac{1}{2}$ *xiii–xx*, seminal grooves straight, joining the prostatic pores in setal line *b* (Fig. 2a). Prostatic pores paired *xvii* and *xix*, each pore being surrounded by a pair of tumid lips.

Male pores paired *xviii*, each midway along a seminal groove.

Female pores closely paired *xiv*, slightly posteriorly to the setal ring within *aa*, distance from setal line *a* equal to *ab*.

Spermathecal pores paired 7/8, 8/9, long, slit-like, extending from within *aa* to $\frac{1}{3}$ *bc*, centre of slit in setal line *b*. Anterior wall of furrow 7/8 lappet-like, directed anteriorly tending to cover the anterior spermathecal pores.

Genital papillae 3 pairs, 13/14, 14/15, 15/16 in setal line *b*.

Internal Characters. First septum 4/5, 4/5–10/11 conical, strongly thickened, 11/12, 12/13 less so. A small pharynx extends to 4/5, the oesophagus from *v–xviii.* Anterior gizzard present *v*, the anterior region being non-muscular ; posterior gizzard *vi.* Oesophageal glands paired, lamelliform *xv–xvii* (3 pairs) ; a separate duct passes into the oesophagus from each gland. Intestine begins *xix*, intestinal caeca present *xxvii–xxx* (4 pairs), occasionally 3 or 5 on one side. Typhlosole ribbon-like, arising *xxvii.*

The dorsal vessel extends posteriorly from the dorsal union of the paired commissural vessels in *vi*. Commissural vessels present *vi–xii* increasing in size posteriorly, all apparently contractile ; they join the dorsal and ventral blood vessels. Supra-oesophageal vessel present between *vi* and the oesophageal glands, segmentally interconnected with the paired commissural vessels.

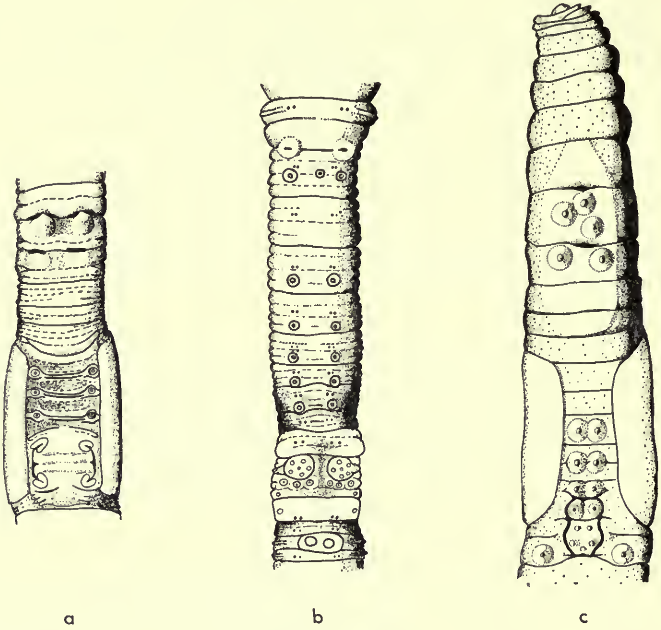

FIG. 2. a.—*Millsonia pumilia*. b.—*M. hemina*. c.—*M. ditheca*. Ventral surface showing genital field.

Testes holandric, funnels paired *x*, *xi*. Each testis is contained in a capsule which is continuous with a lateral horn of the funnel of its side. The ental ends of the funnels are fused medially. Seminal vesicles paired *xi*, *xii*, superficially racemose in appearance, septum 12/13 is slightly distended posteriorly by the bulk of the hinder vesicles. Vasa deferentia paired *xi* and *xii*, each passes into the parietal wall and joins with the other of its side to form a single duct. The ducts may be seen passing posteriorly beneath the lining peritoneum by setal line *b*. Each emerges briefly in *xvii* and passes laterally around the slender, ectal portion of the prostate before leading into the parietes.

Prostates paired, *xvii*, *xiv*, tubular, folded in one or two simple loops or fairly straight extending posteriorly, perhaps to *xl*. The ectal region of each prostate is modified as a slender duct.

Ovaries closely paired *xiii* ; situated on the posterior surface of septum 12/13 near to the ventral parietes. Funnels closely paired seen near to the ventral parietes anteriorly to septum 13/14.

Spermathecae paired, *viii*, *ix*, the posterior pair being larger. Each spermatheca comprises an ampulla and flexed duct of almost equal length. The duct has two diverticula, firstly a rounded, sac-like, ectal diverticulum and secondly about $\frac{1}{3}$ distance from the ectal end, a somewhat pollex-shaped diverticulum. The ampulla is simple but irregularly shaped (Fig. 3b).

Genital papillae seen internally as ovoid, glandular masses on the parietes.

Plectonephridia present as paired tufts laterally to the ventral trunks in the anterior segments as far as *xx*. Meronephridia present, three pairs in each segment from *xiii* onwards.

REMARKS. Compared with other quadrithecal, quadriprostatic species of *Millsonia* this new species may be distinguished mainly by its small size and the presence of only three pairs of intestinal caeca (see Key, p. 299).

Millsonia hemina sp. nov.

2 clitellate, 4 aclitellate specimens. ?Apapam, Ghana. Date? Holotype, British Museum (Natural History) Register No. 1964.2.20 ; paratypes British Museum (Natural History) Register No. 1964.2.21/25.

DIAGNOSIS. *External Characters.* Length 67–139 mm., diameter 1.5–3 mm. Segments 128–161. ? pigmented. First dorsal pore 9/10. Prolobous. Setae small, ventral, closely paired. Genital and penial setae absent. Clitellum *xiii*–$\frac{1}{2}$*xviii* (7$\frac{1}{2}$ segments), saddle-shaped. Male pores paired, united with paired prostatic pores *xvii* (prostatic pores absent *xiv*). Female pores paired *xiv*. Spermathecal pores paired 7/8 in setal line *b*. Genital papillae paired *viii*, *x*–*xiv* (6 pairs) in setal line *b*, paired *xiv* within *aa*.

Internal Characters. First septum 4/5, 4/5–11/12 thickened. Gizzards *v*, *vi*. Oesophageal glands paired *xv*–*xvii*. Intestine begins *xix*, intestinal caeca *xxv*, *xxvi* (2 pairs). Typhlosole ribbon-like, arising *xxiii*. Last lateral hearts *xii*. Holandric, testes paired in testes sacs, *x*, *xi*. Seminal vesicles paired *xi*, *xii*. Prostates paired *xvii* only, tubular, convoluted. Ovaries paired *xiii*. One pair spermathecae only *viii* ; duct with ectal diverticulum and another midway along length ; ampulla simple. Meronephridial.

DESCRIPTION. *External Characters.* Length 67–139 mm., diameter 1·5–3 mm. Segments 128–161. The caudal region (circa *cxl* onwards) of the hototype is quadrangular in cross-section. Cuticle with pale green iridescence. Epidermis ? pigmented (specimens flesh colour, preserved in alcohol). First dorsal pore 9/10. Prostomium prolobous. Most anterior segments tetrannulate, particularly the ventral surface anteriorly to the clitellum ; posteriorly to the clitellum the segments are triannulate, the middle annulus bearing the setae being slightly raised.

Setae small, closely paired. Setal formula at *x* aa : ab : bc : cd = 9 : 1 : 5 : 1, *dd* = $\frac{3}{4}$ circumference ; at *xxx* 6 : 1 : 4 : 1, *dd* = $\frac{3}{4}$ circumference. Genital and penial setae absent but ventral setae somewhat stouter in the pre-clitellar region.

Clitellum saddle-shaped, *xv*–$\frac{1}{2}$*xviii* ventrally, *xiii*–*xvii* dorsally. Genital field, shield-shaped. Male and prostatic pores combined *xvii* in setal line *a*. Each pore issues from a large papilla with three smaller, supernumerary posterior papillae (Fig. 2b).

Female pores paired crescentric slits *xiv*, almost midway between setal lines *a* and *b*, anteriorly to the setae.

Spermathecal pores paired 7/8 in setal line *b*, small, transverse slits surrounded by a slightly raised, swollen circular area.

Genital papillae unpaired *viii* within *aa* otherwise paired *viii* between 2nd and 3rd annuli laterally to seta line *b*, *x–xiv* (5 pairs) between 3rd and 4th annuli in setal line *b*, *xiv* in middle annulus within *aa*.

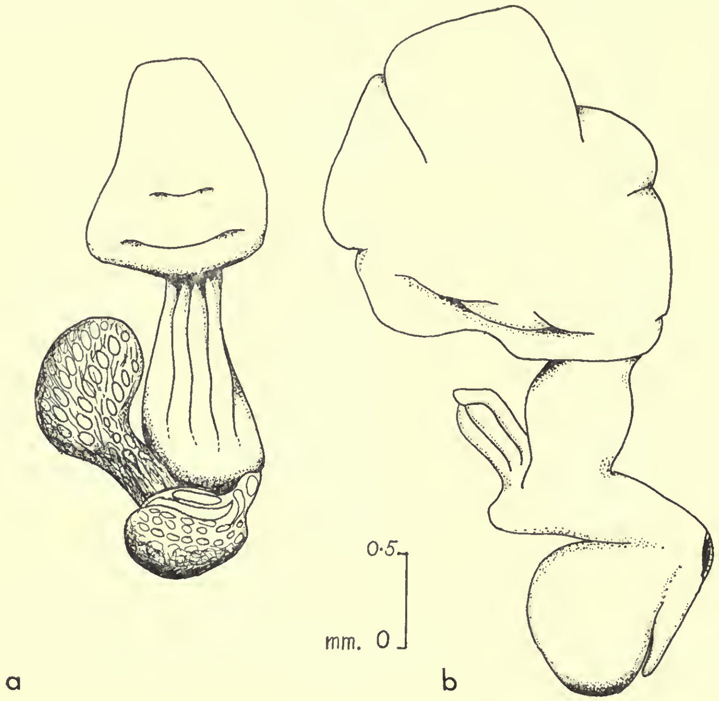

FIG. 3. Antero-dorsal view. a.—*Millsonia hemina* right spermatheca ; b.—*M. pumilia*, posterior spermatheca.

Internal Characters. First septum 4/5, 4/5–11/12 thickened, 12/13, 13/14 less so ; 4/5–7/8 strongly conical. A muscular pharynx extends to septum 4/5 ; anterior gizzard present in *v*, posterior gizzard in *vi*. The gizzards are approximately the same size, the anterior region of each is thin walled. Oesophageal glands lamelliform, paired *xv–xvii* (3 pairs), the anterior pair being slightly smaller than the others ; each gland is joined to the oesophagus by a separate duct. Intestine begins *xiv*, intestinal caeca present *xxv*, *xxvi* (2 pairs). Typhlosole ribbon-like, arising *xxiii*.

The dorsal blood vessel passes anteriorly to *v* where it terminates at the dorsal union of the paired commissural vessel of that segment. Paired commissural vessels present *v–xii*, contractile as functional lateral hearts *x–xii* (3 pairs), joining the dorsal and ventral trunks.

Testes, holandric, paired *x*, *xi*, contained within closely paired testes-sacs extending from the sperm funnels and communicating with the seminal vesicles. Seminal vesicles paired, *xi*, *xii*, small. The two pairs of vasa deferentia unite to form a single duct on each side which passes posteriorly to *xvii*. Each duct lies on the ventral parietes and is seen as a loosely convoluted tube. Prostates, one pair only, tubular, highly convoluted lying along side the anterior region of the intestine. The ectal portion of each prostate is muscular and passes anteriorly to *xvii* where it leads into the parietes together with the vas deferens of its side.

Ovaries paired *xiii*, large, pendent from the posterior surface of 12/13 near to the ventral trunks. Funnels paired, large, each leading into a wide oviduct which passes into the parietes between setal lines *a* and *b*.

Spermathecae, one pair only, *viii*. The diameter of the ampulla is about twice that of the duct which has two diverticula of unequal size (Fig. 3a).

Excretory system combined plectonephric and meronephric. Segments anteriorly to *xii*, tufts of small nephridia clustered around the oesophagus. Meronephridia present from *xiii*, six pairs present in each segment, the lateral pairs being largest.

REMARKS. This species is readily distinguishable from other species of the genus by the presence of only one pair of spermathecae opening into furrow 7/8, one pair of prostates and the fusion of the (paired) prostatic and male pores on *xvii*. Like *pumilia* it is a small *Millsonia* and further resembles this species by the small number of intestinal caeca and the presence of two diverticula on the spermathecal duct.

Millsonia ghanensis sp. nov.

Holotype : clitellate specimen, by side of deep river in stiff wet mud, Bunso, 14th May, 1954. Paratypes 20 clitellate specimens, Bunso, 22nd February 1951. Holotype, British Museum (Natural History) Register No. 1964.2.26 ; paratypes, British Museum (Natural History) Register No. 1964.2.27–46.

Other material : 11 aclitellate specimens, Bunso, 14th May, 1954. 59 aclitellate specimens, Bunso 22nd February, 1951. 19 aclitellate specimens, Bunso, 21st February, 1952. 4 clitellate, 6 aclitellate specimens, along road between Bunso and Kili, 21st February, 1952. 8 aclitellate specimens, Tafo, 8th May, 1955. 15 aclitellate specimens, grounds of Prempeh College ; mud in banks of R. Wiwi (tributary of the R. Oda which flows into the R. Osin), Kumasi, 21st March, 1956. 1 aclitellate specimen, no data.

DIAGNOSIS. *External Characters*. Length 210–387 mm., diameter 9 mm. Segments 262–393. Unpigmented (in life, clitellum bright orange, preclitellar region vivid pink). First dorsal pore ? 12/13, 13/14. Prolobous. Setae ventral, closely paired. Genital and penial setae absent. Clitellum $\frac{1}{2}$ *xiii*–$\frac{1}{2}$ *xx* (7 segments), saddle-shaped. Male pores paired *xviii*. Prostatic pores paired *xvii*, *xix* in setal line *b*. Female pores closely paired within setal lines *aa*. Spermathecal pores paired $\frac{2}{3}$ *vii*, $\frac{2}{3}$ *viii* in setal line *b*. Genital papillae closely paired 9/10–15/16 (7 pairs), 21/22–24/25 (4 pairs) within setal lines *aa*.

Internal Characters. First septum 4/5, 4/5–11/12 strongly thickened, conical, 12/13 less so. Gizzards, $\frac{1}{2}$ *v*, *vi*. Oesophageal glands paired *xv*, *xvi*, *xvii*. Intestine begins *xix*, intestinal caeca *xxvii*–*xxxiii* (7 pairs). Typhlosole ribbon-like, begins *xxvii*. Lateral hearts *x*–*xiii*. Holandric, testes paired *x*, *xi*, in testis sacs ; seminal vesicles paired, *xi*, *xii*, small. Prostates paired, tubular, *xvii*, *xix*. Ovaries paired *xiii*. Spermathecae paired *viii*, *ix*, adiverticulate. Meronephridial.

Description. *External Characters.* Length 210–387 mm., diameter 9 mm. at *x*, 5 mm. at *xx*. Segments 262–393. Cuticle with slight green iridescence. Colour: preserved specimens, pale straw, epidermis unpigmented ; in life, clitellum bright orange, preclitellar region vivid pink. First dorsal pore ?12/13, 13/14. Prostomium large, prolobous.

Setae ventral, closely paired. Setal formula at *x aa* : *ab* : *bc* : *cd*=4 : 1 : 3 : 1, *dd*=$\frac{2}{3}$ circumference ; at *xv* 3·5 : 1 : 2 : 1, *dd*=$\frac{2}{3}$ (setal pairs somewhat more widely spaced) ; at *c* 6 : 1 : 4 : 1, *dd*=$\frac{2}{3}$ circumference.

Segment *v* biannulate ; *vi*, *vii* triannulate ; *viii–xi* tetrannulate ; *xii–xv* pentannulate ; postclitellar region triannulate. Clitellum indistinct, ? saddle-shaped, $\frac{1}{2}$ *xiii*–$\frac{1}{2}$ *xx* (7 segments) extending ventrally nearly to setal lines *dd*. Genital field poorly developed, $\frac{2}{3}$ *xvi*–$\frac{1}{3}$ *xx* ; seminal grooves laterally convex, joining the prostatic pores of each side in setal line *b*.

Male pores paired *xviii*, in the seminal grooves, apparently in setal line *b* (*xvii–xix* setae *b* absent, setal lines *cd* displaced laterally).

Female pores closely paired *xiv* within setal lines *aa*, situated slightly anteriorly to the setal ring ; distance from setal line *a* being nearly equal to *ab*.

Spermathecal pores large, paired $\frac{2}{3}$ *vii*, $\frac{2}{3}$ *viii* within setal lines *ab*. Pores separated from the posterior furrows by 1 annulus, annuli adjacent to the pores, swollen.

Genital papillae closely paired 9/10–15/16 and 21/22–24/25 within setal lines *aa*. Within the genital field, indistinct, paired genital markings.

Internal Characters. First septum 4/5, 4/5–11/12 strongly thickened, conical, 12/13 less so.

Pharynx small, extends posteriorly to 4/5. A small portion of undifferentiated oesophagus in *v* precedes a small anterior gizzard extending to 5/6, large posterior gizzard in *vi* displaces septum 6/7 posteriorly against 7/8. An unpaired, oesophageal pouch is also present in *vi*, it is small and thin-walled and situated median dorsally. Oesophageal glands paired *xv*, *xvi*, *xvii* ; anterior smallest, posterior pair largest. Intestine begins *xix*, wide anteriorly and pouch-like due to intersegmental constrictions *xx–xxvi*. Intestinal caeca present, digitiform, small *xxvii–xxxiii* (7 pairs). Typhlosole begins in *xxvii* as a double fold pendent from the median dorsal line of the interior of the intestine ; when separated the folds are seen to be ribbon-like.

The dorsal blood vessel extends posteriorly from the dorsal surface of the pharynx, anteriorly it is slender but increases in diameter as it passes over the dorsal surfaces of the gizzards and reaches its greatest size in *xiv*. Commissural vessels seen *vii–xiii*, contractile as functional lateral hearts *x–xiii*. The commissural vessels join the dorsal and ventral blood vessels. Anteriorly the ventral vessel is clearly seen lying on the ventral nerve cord but in the segments bounded by thickened, conical septa, it is partly enclosed in the thickened tissue of the septa for most of the length of these segments. A supraoesophageal blood vessel passes posteriorly from *vii–xiii* with segmentally paired branches to the commissural vessels. In *xiv* the supraoesophageal vessel bifurcates and each branch passes into a loose plexus of blood vessels interconnecting the oesophageal glands in *xv–xvii*. A suboesophageal blood vessel was not seen.

Testes holandric, closely paired in sacs immediately below the oesophagus on the posterior surfaces of septa 9/10, 10/11 ; funnels situated on the anterior surfaces of septa 10/11, 11/12 respectively near to the ventral nerve cord. These septa are strongly conical so that the funnels appear to lie on the ventral wall of the segment. Seminal vesicles paired *xi*, *xii*, small ; seen as depressed granular pouches arising from the posterior surfaces of septa 10/11, 11/12. Vasa deferentia are difficult to trace, the two pairs apparently remain separate on each side. Prostatic glands paired *xvii*, *xix*, tubular, long, highly convoluted except for a straight muscular, ectal portion. The prostates enter the parietes a short distance from the ventral nerve cord.

Ovaries paired, *xiii*, free, funnels small, oviducts not seen.

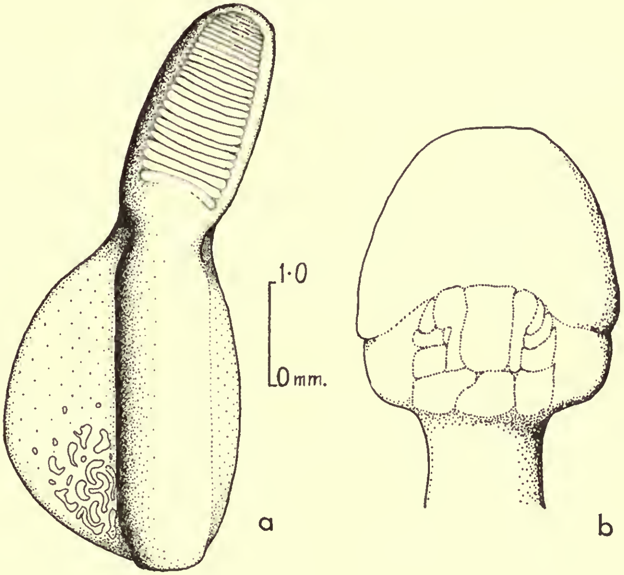

FIG. 4. Posterior spermathecae. a.—*Millsonia ghanensis*, antero-dorsal view ; b.—*M. ditheca*, ventral view.

Spermathecae paired, *viii*, *ix*, the ducts pass obliquely into the parietes by the anterior septum of the segment. Each is digitiform but a slight constriction between the ampulla and duct gives a somewhat clavate appearance. A fin-like process is present along the lateral surface of each duct (Fig. 4a), also the medial surface in riper individuals. The fins are semitransparent and numerous small, vesicular diverticula may be seen through the tissue. Posterior spermathecae slightly larger than the anterior pair.

Excretory system meronephridial. Anteriorly tufts of small nephridia are clustered on the anterior surfaces of the septa near to the oesophagus, posteriorly from *xiv* they are situated on the perietal wall in a single lateral row in each segment. First pair of larger meroneophridia present in *xix*.

Remarks. In comparison with other large, western African, tetrathecate species of *Millsonia*, this new worm is slenderer in general proportions. It may be readily distinguished externally by the arrangement of the closely paired genital papillae. Excluding the region of the genital field, each pair of papillae is situated intersegmentally on a single, raised, oval area ; a raised oval area occurs in each furrow from 9/10 to 24/25 (in less well-developed individuals the papillae are present only in furrows 9/10 to 15/16). Internally, the strongly thickened anterior septa, 4/5–11/12 and to some extent 12/13, and the short series of intestinal caeca, *xxvii–xxxiii* (7 pairs), also serve to distinguish the species.

Millsonia ditheca sp. nov.

1 clitellate, 17 aclitellate specimens, soil beneath cocoa trees, Tafo, 26th October, 1955. 1 clitellate specimen, Tafo, 17th October, 1952. Holotype, British Museum (Natural History) Register No. 1964.2.170 ; paratypes, British Museum (Natural History) Register No. 1964.2.171–188.

Diagnosis. *External Characters.* Length 128, 140 mm., diameter 4·5, 5 mm. Segments 264, 272. Unpigmented. First dorsal pore ?10/11, 11/12. Prolobous. Setae small, ventral, closely paired. Genital and penial setae absent. Clitellum *xiii–xvii* (5 segments), saddle-shaped. Male pores paired *xviii*. Prostatic pores very closely paired *xvii*, *xix*. Female pores closely paired *xiv*. Spermathecal pores single, median ventral, 7/8, 8/9. Anterior genital papillae irregular *viii*, *ix* ; posterior genital papillae paired *xv–xix*.

Internal Characters. First septum 4/5, 4/5–12/13 thickened. Gizzard *vi*. Oesophageal glands paired *xv–xvii*. Intestine begins *xix*, intestinal caeca *xxvii–xxxiv* (8 pairs). Typhlosole ribbon-like, arising *xxviii*. Lateral hearts *x–xii*. Holandric, testes paired in sacs *x*, *xi*, small, funnels short but wide ; seminal vesicles paired, *xi*, *xii*, small. Prostates paired, tubular, *xvii*, *xix*. Ovaries paired, *xiii*. Spermathecae, single, *viii*, *ix*, adiverticulate, passing around either right or left side of ventral trunks, posterior spermatheca larger. Meronephridial.

Description. *External Characters.* Length 128, 140 mm., diameter 4·5, 5 mm. Segments 264, 272 (clitellate specimens). Cuticle with slight blue-green iridescence ; epidermis unpigmented, general colour creamy white, darker posteriorly where the gut-contents may be seen through the gut and body walls, clitellum orange-brown (specimens preserved in alcohol). First dorsal pore ?10/11, 11/12, not seen in the clitellar segments. Prostomium prolobous. Segments tetrannulate in the preclitellar region with the first and fourth annuli narrower than the second and third, strongly triannulate posteriorly to the clitellum.

Setae small, ventrally situated, very closely paired. Setal formula at *x* and *xv* *aa* : *ab* : *bc* : *cd*=4 : 1 : 3 : 1, $dd=\frac{4}{5}$ circumference ; at *c* 7 : 1 : 4 : 1, $dd=\frac{4}{5}$ circumference. Setae near spermathecal pores undifferentiated. Penial setae absent.

Clitellum saddle-shaped, *xiii–xvii* (5 segments) extending ventrally almost to setal line *b*. Genital field small, restricted to *xvii–xix*, intersegmental furrows indistinct ; seminal grooves paired, sinuate, joining the prostatic pores of each side.

Male pores paired *xviii*, each being situated in a seminal groove at the point of intersection with a lateral (? intersegmental) furrow (Fig. 2c). Prostatic pores very closely paired in *xvii* and *xix*, each pair opens into a lateral furrow near to the midventral line.

Female pores closely paired *xiv*, situated in the setal ring within *aa*, distance from *a*=*ab*.

Spermathecal pores single, median ventral in furrows 7/8, 8/9. Ventral surface of $\frac{2}{3}$ *vii–ix* swollen. Anterior genital papillae irregularly arranged, 2 on *viii*, 3 on *ix*, ventrally within setal lines *cc*. Posterior genital papillae paired, *xv* in setal line *b*, *xvi, xvii, xviii* in setal line *a*, *xix* in setal line *d* (Fig. 2c).

Internal Characters. First septum 4/5, 4/5–12/13 thickened, 11/12 and 12/13 only moderately thickened.

A large pharynx extends posteriorly to 5/6, strongly muscular in posterior region of *v* ; oesophageal gizzard *vi*. The oesophagus extends to *xviii* with paired lamelliform oesophageal glands in *xv, xvi, xvii* ; the septa of these segments are slightly displaced anteriorly, the anterior pair of glands occupying part of *xiv*. A duct issues from the hilus of each gland and passes into the oesophagus. The intestine begins in *xix*, paired intestinal caeca present *xxvii–xxxiv* (8 pairs) decreasing in size posteriorly. (Anteriorly to the caeca, *xix–xxvi*, the intestine is slightly dilated segmentally into a series of paired, thin-walled pouches). Typhlosole ribbon-like, arising in *xxviii* ; it is attached along the centre of its dorsal surface to the mid-dorsal line of the internal surface of the gut. In the region of the intestinal caeca the width of the typhlosole is equal to nearly one-third of the circumference of the intestine, posteriorly to this region it is slightly narrower and equal to about one quarter of the circumference.

The dorsal blood vessel extends posteriorly from the dorsal surface of the pharynx in *iv*, paired commissural vessels join it with the ventral blood vessel in *vi–xii*, functional as lateral hearts only in *x–xii*. The ventral blood vessels leads posteriorly from the ventral surface of the pharynx in *iv*. A median supraoesophageal blood vessel extends posteriorly from *vi* with paired branches interconnecting it segmentally with the paired commissural vessel and dorsal blood vessel. It passes posteriorly along the dorsal surface of the oesophagus to *xvii* where a median branch enters the dorsal blood vessel, then in *xviii* the main trunk appears to enter the dorsal blood vessel.

Testes holandric and funnels paired, *x, xi*. Testes small, enclosed in vesicles pendent from the posterior surface of the anterior septum of *x* and *xi* ; situated near to the ventral trunks being almost sub-oesophageal. Funnels truncate but wide, also near to the ventral trunks. Seminal vesicles small, paired *xi, xii*, granular in appearance. A single pair of vasa deferentia lie on the parietes near to the ventral nerve cord, passing posteriorly to *xviii* where the ducts enter the parietes. Prostates tubular, paired *xvii, xix*, loosely coiled entering the parietes latero-ventrally to the nerve cord.

Ovaries small, paired *xiii*, funnels and oviducts not seen.

Spermathecae single, median ventral *viii, ix*, the posterior spermatheca being twice the size of the anterior one. Each consists of a large, simple, pyriform ampulla and squat, adiverticulate duct (Fig. 4b). Both lie slightly to one side of the vertical median plane and each duct curves around and slightly displaces the ventral trunks to enter into the parietes in the mid-ventral line by septa 7/8 and 8/9 respectively. The spermathecae may curve around the right or left side of the ventral trunks.

Internally the genital papillae are seen as ovoid, glandular masses in the parietes.

Excretory system meronephridial. Tufted nephridia grouped medially on the septa of *iv–xi*. From *xii* posteriorly, meronephridia distributed laterally in two regular rows on the parietal wall of each segment ; from *xix* posteriorly, each nephridium comprises a simple loop, terminal vesicle absent.

REMARKS. The median ventral, unpaired spermathecae in furrows 7/8 and 8/9 clearly distinguish *ditheca* from all other known species of *Millsonia*. Although *M. eudrilina* (Cognetti, 1909) was described with one unpaired spermatheca this new species appears, from description, to be closer to the tetrathecate *M. anomala* Omodeo, 1955, from the Ivory Coast. It differs from the latter species mainly on the number of spermathecae and intestinal caeca.

M. ditheca shows some affinities with species of *Wegeneriella* Michaelsen, a genus not recognised by Pickford (1937 : 80) on the grounds that it is a heterogenous assemblage containing convergent species. The main generic characters of *Wegeneriella* are the presence of unpaired spermathecae and two pairs of oesophageal glands in *xiv* and *xv*. In *M. ditheca* the oesophageal glands in *xv* appear superficially to be double and occupy part of *xiv* but as there are also separate paired glands in *xvi* and *xvii* in addition to the presence of intestinal caeca and a broad, ribbon-like typhlosole, I place this species in *Millsonia* Beddard, sensu Omodeo (1955 : 218).

REMARKS ON THE GENUS *MILLSONIA*. The new species of *Millsonia* described above further extend our knowledge of the range of morphological variation in the genus (Omodeo, 1958 : 59). Until now species of *Millsonia* have been regarded as containing large individuals but with the descriptions of *hemina* and *pumilia* come the first details of small worms. It is interesting to note, moreover, that there are few intestinal caeca in these species, particularly, in the smaller, *hemina*, where there are only two pairs, *xxv*, *xxvi*, whereas in the much larger *caecifera* (Benham) there is a series of 24 pairs, *xxix–lii*.

The number of spermathecae is variable in *Millsonia*, the tetrathecate condition is the commonest and is, presumably, the primitive condition of the genus. However, the anterior pair of spermathecae are wanting in *mimus* (Michaelson), *nigra* Beddard and *sokodeana* (Michaelson) while in *eudrilina* (Cognetti) there is only one spermathecal pore being median ventral in furrow 8/9. Now two other conditions have been found, in *hemina* the posterior pair of spermathecae are wanting (functionally this condition may be correlated with the reduction in the number of prostates) and in *ditheca* there are two unpaired, median ventral spermathecae in furrows 7/8, 8/9.

In the new species described above it would seem that most variations are independent of others although, as already mentioned, some are apparently correlated, e.g. the two smallest species, *hemina* and *pumilia*, have the least number of intestinal caeca. Generally all of these new worms would seem to consist of a mosaic of primitive and specialised characters. In the case of the tiny *hemina*, the most obvious feature is the small size, a character which is usually regarded as a criterion of a less specialised condition, yet the spermathecal and male reproductive systems are highly modified. In the absence of palaeontological evidence and knowledge of the rates of evolution of species and organ systems, I do not propose to follow fallacious precedents and arrange the species in a phylogenetic sequence on the morphological complexity of one organ system, e.g. nephridia.

The worms collected by Miss Tazelaar do not extend the known range of *Millsonia*, in fact, Ghana appears to be about the centre of the distribution of the genus. Omodeo (1955 : 217) figured a map showing every locality where specimens of each species of *Millsonia* had been collected, from this it is clear that the genus is confined to the rain forests in western Africa south of the River Niger.

Genus ***Millsonia*** Beddard

KEY TO SPECIES, AFTER OMODEO, 1958 : 59

1	Spermathecal pores in or near furrow 7/8 *and* 8/9	2
–	Spermathecal pores in furrow 7/8 *or* 8/9	10
2	Spermathecal pores single (median ventral 7/8 and 8/9)	***M. ditheca*** sp. nov.
–	Spermathecal pores paired	3
3	Penial setae present, tusk-like, pitted (genital papillae absent, ducts of spermathecae fused together and with parietal wall)	***M. schlegeli*** (Horst, 1884)
–	Penial setae absent	4
4	Genital papillae absent (anterior and posterior spermathecae of equal size)	***M. insignis*** (Michaelsen, 1922)
–	Genital papillae present	5
5	Last lateral hearts in segment *xii*	6
–	Last lateral hearts in segment *xiii*	8
6	1 gizzard present (segment *vi*)	***M. anomala*** Omodeo, 1955 : 219
–	2 gizzards present (segments *v* and *vi*)	7
7	Intestinal caeca numerous, *xxix–lii* 24 pairs, (body length long, circa 500 mm.)	***M. caecifera*** (Benham, 1894)
–	Intestinal caeca few, *xxvii–xxx* 4 pairs, (body length short, circa 100 mm.)	***M. pumilia*** sp. nov.
8	14–15 pairs of intestinal caeca, *xxx–xliii*, *xliv* ; (spermathecal pores in setal lines *c*)	***M. inermis*** (Michaelsen, 1892)
–	7 pairs of intestinal caeca	9
9	Intestinal caeca *xxvii–xxxiii* (spermathecal pores in setal lines *b*)	***M. ghanensis*** sp. nov.
–	Intestinal caeca *xxxvi–xlii* (spermathecal pores in setal lines *d*)	***M. heteronephra*** (Michaelsen, 1897)
10	Spermathecal pores in furrow 7/8	***M. hemina*** sp. nov.
—	Spermathecal pores in furrow 8/9	11
11	Spermathecal pore single, median ventral	***M. nigra**** Beddard, 1894
—	Spermathecal pores paired	12
12	Prostatic pores between setal lines *ab* (diameter of body circa 12 mm.)	***M. mimus*** (Michaelsen, 1891)
—	Prostatic pores between setal lines *bc* (diameter of body circa 4 mm.)	***M. sokodeana*** (Michaelsen, 1913*a*)

**Minigra* Beddard, 1894 and *M.eudrilina* (Cognetti, 1909) are synonymous (Sims, *in prep.*).

EUDRILIDAE

Libyodrilus sp.

Libyodrilus: Clausen, 1965. Vidensk. Medd. fra Dansk naturh. Foren., **128** (in press).

7 clitellate, 5 aclitellate specimens ; Ho, south eastern Ghana, 29th December, 1957.

Description. *External Characters.* Length 106–132 mm., diameter 4–4·5 mm. Segments 159–174 (clitellate specimens). Colour pale greyish flesh above, whitish grey below, clitellum lilac ; cuticle with slight bluish green iridescence and pink reflections (specimens preserved in alcohol). Dorsal pores absent. Prostomium prolobous.

Clitellum annular extending over nearly four segments, $\frac{1}{3}$ *xiv*–$\frac{2}{3}$ *xvii*. Setae lumbricine, closely paired, ventrally situated. Setal formulae at *x* $aa : ab : bc : cd :$ $=6 : 1 : 4 : 1$, $dd=\frac{3}{4}$ circumference ; at *xv* $4 : 1 : 3 : 1$, $dd=\frac{3}{4}$ circumference ; at *xxx* $6 : 1 : 4 : 1$, $dd=\frac{3}{4}$ circumference. Paired penial setae 1·04 mm. long present on the male papilla, each is slightly curved distally.

Male pore single, median ventral in furrow 17/18, raised on a small setose papilla extending $\frac{2}{3}$ *xvii*–$\frac{1}{3}$ *xviii*.

Female pores inconspicuous, paired, *xiv* near furrow 14/15, dorsally to setal line *d* at distance of 5*cd*.

Spermathecal pore single, median ventral in *xiii* as a small transverse slit slightly posteriorly to the setal ring.

Nephridiopores paired, inconspicuous, in the posterior wall of each furrow, dorsally to setal line *d* at distance 4*cd*.

Internal Characters. First septum 5/6, 5/6–11/12 thickened ; all septa in the preclitellar region are strongly conical. The buccal cavity opens into a muscular pharynx extending into *iv*, the oesophagus passes posteriorly from *v* to *xix* where the intestine begins ; oesophageal gizzard, glands and appendages absent. The first four segments of the intestine, *xix–xxii*, form a thin-walled crop which is followed by three gizzards in *xxiii–xxv* with thin-walled intersegmental pouches in 23/24 and 24/25. A low typhlosole begins in *xxviii* as a small longitudinal ridge along the dorsal surface of the lumen of the intestine.

Paired lateral hearts in *vi–xii*, these commissural vessels are long and somewhat convoluted, the more posterior pairs are stouter and ? more strongly contractile ; any pair may be inequally developed. The commissural vessels join the dorsal and supraoesophageal blood vessels with the ventral blood vessel. The dorsal blood vessel extends posteriorly from the dorsal union of the paired commissural vessel in *vi*, from *xii–xxi*, ?*xxii* it is bifurcated segmentally but reunites to pass through the septa, appearing as a series of rings. The supraoesphageal blood vessel extends posteriorly from the pharynx to septum 12/13 where it enters the dorsal blood vessel. The sub-oesophageal blood vessel passes along the ventral surface of the oesophagus from the pharynx to *xii* where it dilates and bifurcates as it passes through septum 12/13 then each branch gives off a side branch to the adjacent lobe of the receptaculum seminis in *xiv–xvi*, the main branches continue posteriorly to the euprostates.

Testes holandric, paired in *x* and *xi* near to the ventral parietes within folds of the posterior surface of septa 9/10 and 10/11. Funnels paired in *x* and *xi*, they are directed anteriorly and seen as large, white-iridescent foliations in the posterior region of the segments laterally to the ventral trunks. Seminal vesicles paired in *xi* and *xii*, small, lobulate. Each vas deferens remains separate and those of each side pass closely together to the (paired) euprostatic gland of its side which it enters about midway along the lateral surface. The euprostates are paired in *xviii*, small and flexed posteriorly they reach only to *xix*. Ectally the two euprostates pass into the ventral parietes adjacent to the ventral trunks between *xvii* and *xviii*, displacing septum 17/18 slightly anteriorly.

Ovaries paired in *xiii*, small, each is enclosed by an ovarian vesicle on the posterior surface of septum 12/13. As the septum is strongly conical the ovaries are situated on a laterally facing surface (Fig. 5), while the medial region of the septum lies within the parietes of *xv*. A short, stout oviduct leads from each ovary to a (paired) ovisac, which communicates with the fertilization chamber. Sperm pass to this chamber from the receptaculum seminis, ectally it narrows and forms an egg duct which passes antero-laterally towards the parietes.

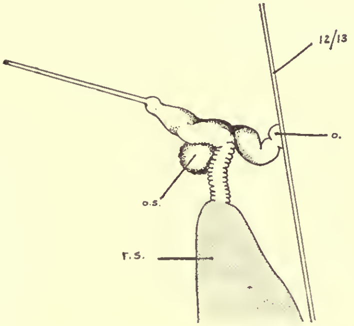

FIG. 5. *Libyodrilus* sp. female reproductive system, left side, dorsal view ; *o.*, ovary ; *o.s.*, ovisac ; *r.s.*, receptaculum seminis ;*12/13*, septum 12/13 (passing obliquely).

The spermathecal system consists of a single receptaculum seminis lying above the oesophagus mainly in *xiv–xvi* with a pair of ventral lobes in each segment. Dorsally to the anterior pair of lobes, a pair of ducts extend antero-ventrally on either side of the oesophagus and the ventral trunks in *xiii*. Medially they are flexed where they meet and pass into the parietes midventrally below the nerve cord. (Due to the posterior displacement of the contents of the coelomic cavity, these anterior horns of the receptaculum join ventrally to the posterior pair of seminal vesicles). The lobes form one large ring around both the oesophagus and the nerve cord and do not coalesce between them. The anterior extremity of each lobe in *xiv* leads into the fertilisation chamber which forms part of the female system.

Excretory system meganephridial ; in those anterior segments containing the lateral hearts, the nephridial tubules are long and much convoluted whereas in the clitellar region the nephridia are small.

REMARKS. This species is placed in the genus *Libyodrilus* Beddard (1891*c*) mainly on the presence of intestinal gizzards and the absence of an oesophageal gizzard, glands or appendages. The specimens from Ho are similar to *L. violaceus* Beddard (syntype examined) (Gates, 1962) but differ mainly in that the anterior horns of the receptaculum seminis form one large ring around both the oesophagus and the nerve cord compared with two separate rings joined by a single, median duct ; they are also slightly smaller. They differ from *L. kamerunensis* Michaelsen, 1915, in the same characters but, in addition, they are holandric like *violaceus* whereas *kamerunensis* is metandric.

Eudrilus buettneri Michaelsen, 1892

Eudrilus buettneri Michaelsen, 1892, Arch. Naturg. esch. **58** : 256 :–Bismarckburg, Togoland.

7 clitellate, 3 aclitellate specimens, roadside, between Bunsu and Kili, 21st February, 1952. 2 clitellate, 9 aclitellate specimens, Tafo, 17th October, 1952. 4 clitellate specimens, Tafo, 14th May, 1954. 1 clitellate specimen, Prempeh College, 21st March, 1956. 2 clitellate specimens, Ho, 28th December, 1957.

DESCRIPTION. *External Characters.* Length 142–171 mm., diameter 4–5 mm. Number of segments 162–198 (8 specimens, remainder damaged). Cuticle with azure blue iridescence ; colour vinous purple above otherwise unpigmented, i.e. pale straw below (specimens preserved in alcohol). Dorsal pores absent. Prostomium epilobous. The clitellum extends over slightly more than four segments, *xiv*–$\frac{1}{3}$ *xviii*, saddle-shaped (Fig. 6a).

The setal arrangement is lumbricine ; setal formulae at *x aa* : *ab* : *bc* : *cd* : *dd*= 5 : 1 : 4 : 1 : 25. dd=$^3/_5$ circumference ; at *xv* 4 : 1 : 3 : 1 : 14, *dd*=$\frac{1}{2}$ circumference ; at *xxx* 6 : 1 : 4 : 1 : 18, *dd*=$\frac{1}{2}$ circumference. Penial setae absent.

Male pores paired in furrow 17/18 as narrow, transverse slits extending laterally from setal line *b*, surrounded by tumid lips with scalloped radial ridges.

Female and spermathecal pores combined, paired in furrow 13/14 extending from midway between setal lines *bc* to line *c*, surrounded by smooth, tumid lips.

Nephridiopores paired, near anterior furrow of each segment, midway between setal lines *c* and *d*.

Internal Characters. First septum 4/5, 7/8–9/10 thickened, 10/11 11/12 less so. The buccal cavity opens into the pharynx which extends to *iv*. An oesophageal gizzard in *v* occupies $\frac{1}{2}$ *v*–*vii* and causes septa 5/6, 6/7 to become conical by displacing them posteriorly against 7/8. The oesophagus extends to $\frac{1}{2}$ *xiii* where the intestine commences. Oesophageal glands are present in *x*, *xi* as unpaired median ventral pouches and in *xii* as a pair of lateral, stalked glands.

Paired lateral hearts in *viii*–*x* join the dorsal and ventral blood vessels ; they also interconnect the supraoesophageal blood vessel with the dorsal blood vessel as it passes between the pharynx and the paired oesophageal glands in *xii*.

Testes holandric, paired in *x* and *xi*, each is enclosed in a testis sac. Near to the oesophagus each testis sac communicates with the seminal vesicle in the succeeding segment. More laterally each sac passes into a modified funnel or sperm sac which leads into a vas deferens. Seminal vesicles paired in *xi* and *xii*, smooth, the hinder pair displaces septum 12/13 slightly posteriorly. Each vas deferens passes posteriorly over the ventral parietes, laterally to the ventral trunks. In *xvii* each is flexed laterally then loops back to enter the ectal end of the euprostatic gland of its side. Euprostatic glands paired, extending from *xvii–xxii* ; in *xviii* the ectal end of each gland is directed posteriorly where it enters the medial surface of the (paired) copulatory chamber, more entally the glands curl laterally or dorsally and pass back to the region of *xxii*. The copulatory chambers are small, simple, domed pouches ; in diameter each is twice the length of the segment and slightly displaces septum 17/18 and 18/19 posteriorly.

The ovaries are paired in *xiii* and lie on the posterior face of septum 12/13 near to the ventral parietes, adjacent to the ventral nerve cord (Fig. 6b). Each is enclosed by a vesicle from which a duct passes postero-laterally to the paired female/spermathecal apparatus and into the ovisac (Michaelsen, 1892 : 257, showed the duct leading into the receptaculum seminis). Each spermathecal system comprises a short atrium leading from the female/spermathecal pore, ectally there are two spherical diverticula, more entally a stout duct leads from the posterior surface into the ovisac and a short slender duct leads from the anterior surface into another spherical diverticulum. Entally a thinner walled receptaculum seminis leads from the atrium, this is long and convoluted and occupies most of the coelomic space available in *xiv*.

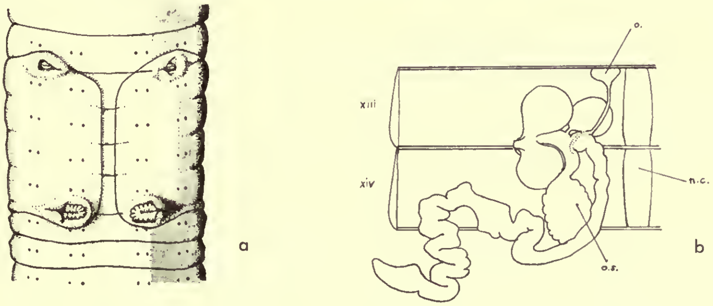

FIG. 6. *Eudrilus buettneri* ; a.—Clitellar region, ventral surface. b.—Female and spermathecal systems, left side, dorsal dissection ; *n.c.*, ventral nerve cord ; *o.*, ovary ; *o.s.*, ovisac.

Excretory system meganephridial, the nephrostome is near to the ventral parietes ; each nephridium is suspended from the anterior septum by a membrane nearly one quarter of the length of the segment. The reservoir of each nephridium is thick-walled and the middle portion of the nephridial duct is highly convoluted.

REMARKS. *Eudrilus buettneri* has been recorded only once, when the unique, aclitellate holotype was described from Bismarckburg, Togoland. The worms fom Tafo agree with the description but many being clitellate, provide further information of the external morphology (the original description is also supplemented with other details of anatomy).

Michaelsen (1900 : 402) placed *E. buettneri* in the synyonymy of *E. pallidus* Michaelsen, 1891, but eventually regarded it as a variety of the latter (1913 : 39). The status of *E. buettneri* is still no clearer ; the present series shows that this worm is widely distributed in south-eastern Ghana also other specimens in the collections of the British Museum (Natural History) come from Aburi, that is, from localities fairly near to Accra from where *E. pallidus* was described. It seems unlikely that the specimens of these taxa are representatives of allopatric populations of the same species in view of the propinquity of the collecting stations. In the absence of evidence of their being ecological representatives, I propose to regard the two taxa as separate species on the differences listed between them by Michaelsen (1913*b* : 42) which I found to be constant in the series examined.

Eudrilus eugeniae (Kinberg, 1866)

Lumbricus eugeniae Kinberg, 1866, Ofvers. Vetensk Akad. Förh. Stockh., **23** : 98 :– St. Helena.

60 clitellate, 11 aclitellate specimens. Aburi, 1st June, 1956.

Hyperiodrilus africanus Beddard, 1891

Hyperiodrilus africanus Beddard, 1891, Quart, J. micr. Sci., n.ser. **32** : 236.

2 clitellate specimens. Prempeh College grounds, Kumasi. 17th November, 1955.

Hyperiodrilus marthae sp. nov.

1 clitellate specimen. Damp soil under roadside grass, Ketekrachi, south-eastern Ghana. 14th February, 1951. Holotype, British Museum (Natural History) Register No. 1963.10.120.

DIAGNOSIS. *External Characters.* Length 96 mm., diameter 3 mm. Segments 202. Unpigmented. Dorsal pores absent. Proepilobous. Clitellum annular. Setae eudriline, $ab > cd$, penial setae absent. Male pore single, median ventral in furrow 17/18. Porophores absent. Female pores paired in anterior wall of furrow 14/15 in line with the nephridiopores. Spermathecal pore single, median ventral *xii* (in posterior wall of furrow 11/12). Nephridiopores paired, midway between setal lines *c* and *d*.

Internal Characters. First septum 4/5, 5/6–10/11 thickened. Oesophageal gizzard absent, intestinal gizzards *xvii–xxiv* (8). Oesophageal glands paired *xiii*, unpaired median ventral pouches *ix, x, xi*. Last lateral hearts *xi, ?xii*. Holandric, testes in testis sacs on posterior septa of *x, xi*. Seminal vesicles small. Euprostates small, leading separately to male pore. Ovaries paired *xiii*, enclosed in ovarian vesicles. (Spermathecal system apparently not fully developed). Meganephridial.

DESCRIPTION. *External Characters.* Length 96 mm., diameter 3 mm. Segments 202. Cuticle, slight yellow-green iridescence ; areas bounded by setal lines *a* and *b*, also *c* and *d* reflect separately from the areas bounded by *a* and *a*, also *b* and *c*.

Colour pale straw, pigment apparently absent (specimen preserved in alcohol). Dorsal pores absent. Prostomium proepilobous. The clitellum is annular and extends over 4 segments, *xiv–xvii*.

Setae eudriline, $ab > cd$. Setal formulae at *x* $aa : ab : bc : cd : dd = 5 : 3 : 5 : 2 : 75$, $dd = \frac{2}{3}$ circumference ; at *xxx* $3 : 2 : 4 : 1 : 50$, $dd = \frac{2}{3}$ circumference (setae *cd* absent in the clitellar region). Penial setae absent.

Male pore single, median ventral in furrow 17/18 on a papilla extending $\frac{1}{2}$ *xvii*–$\frac{1}{2}$ *xviii*, the posterior border of the papilla being lappet-like (Fig. 7a).

Female pores paired in near the anterior wall of furrow 14/15 in the line of the nephridiopores (setae *cd* missing in *xiv*, *xv*).

Spermathecal pore single, median ventral, small, slightly swollen transverse slit in the posterior wall of furrow 11/12 i.e. in *xii*.

Nephridiopores paired in the posterior wall of each furrow midway between setal lines *c* and *d*, starting in 2/3.

Internal Characters. First septum 4/5, 5/6–10/11 thickened, first five septa strongly conical, the next four less so. The buccal cavity opens into the pharynx extending to *v*. The oseophagus extends to *xiii*, the intestine commences in *xiv*. The first three segments of the intestine from *xiv–xvi* are dilated to form a crop, a series of eight intestinal gizzards is present in *xvii–xxiv*. Oesophageal calciferous glands are present as unpaired, median ventral pouches in *ix*, *x*, *xi* and as paired lateral ducted glands in *xiii*.

Paired lateral hearts are present *vi–xi*, a paired non-contractile, commissural vessel is also present in *xii* ; these pass from the dorsal to the ventral blood vessels with interconnections with the supra-oesophageal vessel. The latter passes along the dorsal surface of the oesophagus between the pharynx and a plexus of blood vessels in *xiii* draining the paired calciferous glands. A suboesophageal vessel passes along the ventral surface of the oesophagus from the pharynx over the median calciferous glands in *ix*, *x*, *xi* and descends in *xii* to form the sub-neural blood vessel.

Testes holandric, paired in *x* and *xi*, each is situated near to the posterior septum of its segment within a U-shaped testis sac. Each sac communicates postero-dorsally with the seminal vesicle of the next segment and ventrally narrows to become a vas deferens before passing posteriorly through the septum. The vasa deferentia remain separate and extend posteriorly along setal line *c* to the euprostate of that side. Both euprostates are directed anteriorly but they are sharply flexed and the ental portion lies dorsally, above the ectal part ; both are 5–6 mm. long. In *xviii* the vasa deferentia pass anteriorly along the lateral surface of each euprostate which they enter in the ental third. Ectally the two euprostates pass into the parietes in the anterior part of *xviii*, laterally to the nerve cord.

The ovaries are paired, each is enclosed in an ovarian vesicle lying on the ventral parietes in *xiii* near to septum 12/13, the lateral apex of the sac being adjacent to the vasa deferentia. The ovarian duct of each side was not seen. (There are several coelomic membranes in the vicinity of the ovarian vesicle forming a number of intra-coelomic chambers, one communicates with the fertilization chamber at the ental end of the oviduct).

The spermathecal system consists of an atrium leading from the parietes at septum 11/12, ectally it is three times the width of the nerve cord but as it passes posteriorly it gradually tapers. In the anterior region of *xiii* the extension of the atrium comes to lie to the left of the ventral nerve cord where a delicate, membranous duct joins it with the left fertilisation chamber ; then with four dorso-ventral flexures it leads across beneath the central nerve cord to near the right fertilisation chamber. Here another delicate membranous duct joins the right chamber with the atrial extension which continues posteriorly and ends blindly by the anterior surface of septum 14/15 (Fig. 7b).

Excretory system meganephridial, one pair of nephridia in each segment commencing in *iii*.

REMARKS. Compared with other species of *Hyperiodrilus*, the position of the spermathecal pore of *H. marthae* is intermediate between that in *H. lagosensis* where it occurs on *xi* and in *H. africanus* on *xiii*, in addition there are more intestinal gizzards. The specimen is not fully adult, the testes and seminal vesicles are small, the spermathecal system is poorly developed and there are no ovarian ducts passing between the ovaries and the fertilisation chambers.

Hyperiodrilus prosothecaporus sp. nov.

1 clitellate specimen. Ho. 28th December, 1956. Holotype, British Museum (Natural History) Register No. 1963.10.121.

DIAGNOSIS. *External Characters*. Length 57 mm., diameter 1·5 mm. Segments 125. Colour (preserved in alcohol) white anteriorly, greyish posteriorly, clitellum cream. Dorsal pores absent. Epilobous. Clitellum annular. Setae eudriline, $ab > cd$. Penial setae absent. Male pore single, mid-ventral 17/18. Female pores paired *xiv*, one quarter of distance from setal line *c* to setal line *d*. Spermathecal pore single, mid-ventral *ix* near furrow 9/10. Nephridiopores paired, midway between setal lines *c* and *d*.

Internal Characters. First septum 4/5, 5/6–10/11 thickened, moderately conical. Nonmuscular oesophageal dilation *v*, intestinal gizzards *xix–xxii* (4). Oesophageal glands single, mid-ventral *ix*, *x*, *xi*, paired, lateral *xiii*. Last hearts *xi*. Holandric, vasa deferentia lead into ental end of euprostates, copulatory pouch present. Ovaries paired *xiii*, paired ovarian duct leads to fertilisation chamber in *xiv*. from where oviduct passes to the exterior. Spermathecal atrium leads posteriorly from *ix* to *xiv* where it enters the perispermathecal sinus which encircles the oesophagus and is connected with the fertilisation chambers. Meganephridial.

DESCRIPTION. *External Characters*. Length 57 mm., diameter 1.5 mm. Segments 125. Cuticle with slight green iridescence. Pre-clitellar region white-cream colour, clitellum cream, post-clitellar region pale grey (specimen preserved in alcohol). Dorsal pores absent. Prostomium epilobous. Clitellum annular, *xiv–xvii* (4 segments).

Setae eudriline, $ab > cd$. Setal formulae throughout, $aa : ab : bc : cd = 2 : 1\frac{1}{2} : 3 : 1$, $dd = \frac{1}{2}$ circumference. Penial setae absent.

Male pore single, small lateral slit, mid-ventral in furrow 17/18 leading into a small copulatory pouch in *xviii* ; pore surrounded by two tumid lips, the anterior lip being formed from part of the posterior region of *xvii* and the posterior lip from part of the anterior region of *xviii*.

Female pores paired *xiv*, near to the posterior margin of the segment by furrow 14/15, situated about one-quarter of the distance from setal line *c* to *d*, i.e. midway between the line of the nephridiopores and setal line *c*.

Spermathecal pore single, midventral, slit-like, apparently forming part of furrow 9/10 but on opening the lips the entrance to the spermathecal atrium is seen to be in *ix*. The lips of the pore are formed partly from the posterior region of *ix* and the anterior region of *x*.

Nephridiopores paired, beginning ?2/3, 3/4. The pore is always situated a short distance posteriorly to the furrow, midway between setal line *c* and *d*.

Genital papillae and markings absent.

Internal Characters. First septum 4/5, 5/6–10/11 thickened, moderately conical. Small buccal cavity opens into a large muscular pharynx extending to *iv*. The oesophagus begins in *v* and passes posteriorly to *xiv*, it is dilated in *v* to form a small, thin-walled, non-muscular chamber. The intestine begins in *xv*, a crop is present *xv–xviii*, in the anterior region of *xix* the intestinal wall is thickened by a chitinoid ring, also in *xx–xxiii*, thus forming a series of 4 intestinal gizzards in *xix–xxii*. Typhlosole rudimentary extending posteriorly from *xxvii*, represented by a slight narrow ridge along the mid-dorsal line of the interior of the intestine. Oesophageal glands present as unpaired, ventral pouches *ix*, *x*, *xi*, the first in *ix* is small and poorly developed. Paired lateral glands present in *xiii*, pouch-like in appearance due to the stalks being short and broad.

Dorsal blood vessel extends anteriorly to the dorsal union of the paired commissural blood vessel in *vi*, reaching its fullest development in the segments anteriorly to the paired oesophageal glands. Paired commissural vessels join it with the ventral vessel in *vi–xi*, all apparently being contractile ; a more slender, paired commissural vessel in *xii* appears to pass from the dorsal vessel to the sub-neural vessel. A supraoesophageal vessel passes between the pharynx and the paired oesophageal glands in *xiii*. The dorsal and supra-oesophageal vessels are interconnected segmentally by paired commissural vessels. A sub-oesophageal vessel leads posteriorly from beneath the pharynx, following the profile of the oesophageal pouches in *ix*, *x*, *xi*. Posteriorly to these segments it is difficult to distinguish this vessel in the preserved specimen but either it, or a branch, passes ventrally to the left side of the ventral nerve cord to become the sub-neural vessel.

Testes holandric paired *x*, *xi*, enclosed in bean-shaped testes sacs pendent from the posterior septum of their segment. A slender duct issues from the dorsal end of each testis sac and passes posteriorly through the septum into the seminal vesicle in the following segment. Seminal vesicles paired *xi*, *xii*, small racemose. A vas efferens leads from the ventral end of each testis sac, it passes obliquely posterio-laterally before flexing and turning posteriorly. The vasa efferentia of each side unite in *xii* to form a single (paired) vas deferens. The paired vas deferens continues posteriorly over the parietal wall to the euprostates. Euprostatic glands paired, *xv–xviii*. The vasa deferentia pass into the ental (anterior) end of the glands which taper ectally, in *xviii*, before turning medially and leading into a single median, depressed copulatory pouch. The copulatory pouch is circular with a diameter almost equal to the distance between septa 17/18 and 18/19.

Ovaries paired, *xiii*, each is enclosed within an ovarian vesicle near to the ventral parietes and pendent from the posterior face of septum 12/13. An ovarian duct passes posteriorly to the ovisac in *xiv* which is joined to the fertilisation chamber in *xiii* (these chambers are closely applied to septum 13/14 which is partly wrapped around the fertilisation chamber and separating it from the ovisac). The oviduct leads posterolaterally from the fertilisation chamber to the parietal wall anteriorly to septum 14/15. A diverticulum is present on the oviduct about one-third of the distance from the fertilisation chamber to the parietes. In length it is about half as long as the oviduct, it is medially directed and its distal end lies close by the ventral nerve cord.

Spermathecal atrium single, ovoid, extending from the hinder part of *ix* to septum 10/11. It continues as a narrower, comparatively thin-walled duct to the anterior region of *xiv* where it bifurcates to form a pair of small lateral horns (Fig. 7c). The horns are enclosed within a small transparent, membranous dome-shaped vesicle

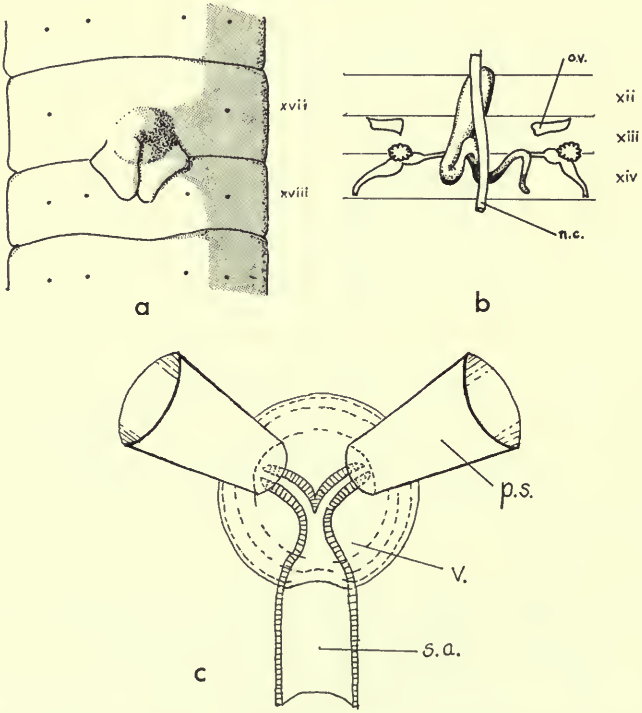

FIG. 7. *Hyperiodrilus marthae* : a.—Ventral surface showing male pore ; b.—Female reproductive and spermathecal systems, dorsal dissection. *ov.*, ovary ; *n.c.*, ventral nerve cord ; c.—*H. prosothecaporus* : diagram, spermathecal vesicle, dorsal dissection. *p.s.* perispermathecal sinus ; *s.a.*, spermathecal atrium ; *v.*, vesicle.

which is continuous with a pair of lateral, perispermathecal sinuses. The sinuses pass from each side of the dome to the fertilisation chambers, then dorsally where they unite to complete a circumoesophageal ring. Spermathecal sac not seen.

Excretory system meganephridial, one pair of meganephridia to each segment ; nephridia uniform throughout the body.

REMARKS. *H. prosothecaporus* may be readily distinguished from all other known species of *Hyperiodrilus* by the anterior position of the spermathecal pore in furrow 9/10. This condition appears to be primitive for it is in the same region as the pore(s) in the Ocnerodrilidae, the family which may represent the grade of structure of a common ancestor, or, as Stephenson (1930 : 864) believed, the family from which the Eudrilidae has actually evolved.

The oesophagus of *H. prosothecaporus* is dilated in segment *v* but the structure is not regarded as forming an oesophageal gizzard since it is thin-walled and non-muscular being apparently of little functional importance. It is, however, of some taxonomic significance and the species has been placed in the genus *Hyperiodrilus* chiefly on this single character. The genus *Legonea* may be distinguished from *Hyperiodrilus* mainly by the presence of a functional oesophageal gizzard in segment *v* (Clausen, 1963 : 2 ; Sims, 1964 : 592). An oesophageal gizzard is present in most other Eudrilid genera and the dilation in the fore-gut of segment *v* of *H. prosothecaporous* could represent a relict structure.

The primitive situation of the spermathecal pore and the presence of a vestigial oesophageal gizzard have not been previously recorded in *Hyperiodrilus* so it could be that this species is a more primitive member of the genus than most, while the vestigial gizzard serves to link *Hyperiodrilus* more closely with *Legonea*. A further resemblance is to be found in the male reproductive system of this species which is moderately specialised in that the male pore opens into a small copulatory pouch similar to that in the somewhat specialised, rather aberrant species *Legonea rapta* in which a penis and copulatory appendages are also present. It is interesting to note that in both *H. prosothecaporus* and *L. rapta*, porophores and genital papillae are absent. In all other species of *Hyperiodrilus* and *Legonea* the male pores are very closely paired at the apex of a V-shaped seminal groove where they are regarded as forming a single pore and there is a porophore at each end of the seminal groove.

The structure of the spermathecal system and its particular stage of development in the specimen described above may provide a solution to the problem of the origin of the perispermathecal sinuses in a species of the closely related genus *Legonea*. *L. modesta* has a spermathecal system almost identical with those of species of *Hyperiodrilus*. In one young specimen of *L. modesta* the spermathecal ducts were found to be little more than buds at the posterior end of the spermathecal atrium, while apart from a small, triangular, membraneous vesicle lying dorsally to the dorsal blood vessel and the oesophagus, there was no trace of the sinuses (Sims, 1964 : 590). It was suggested that the sinuses may be derived by differentiation of the existing coelomic membranes or from the peritoneum which could form a sheath to the inthrusting, developing spermathecal ducts. This present specimen apparently represents the next stage in the development of the perispermathecal sinuses. It shows clearly that they are formed entirely from coelomic membranes. This is evident since the sinuses encircle the oesophagus, extending from the posterior end of the atrium to where they unite above the dorsal blood vessel, yet the spermathecal ducts extend only a short distance from the atrium (Fig. 7*c*). The late development of the ducts also indicates that they do not act as organisers and induce the differentiation of the coelomic membranes into the perispermathecal sinuses.

Genus ***Hyperiodrilus*** Beddard

KEY TO SPECIES

	Intestinal gizzards	Spermathecal pore Segment No.
prosothecaporus sp. nov.	*xix–xxii* (4)	*ix* (near 9/10)
millsoni (Beddard, 1893)	*xviii–xxii* (5)	*x*
lagosensis (Beddard, 1891)	*xviii–xxiii* (6)	*xi*
marthae sp. nov.	*xvii–xxiv* (8)	*xii* (near 11/12)
africanus Beddard, 1891	*xvi–xxii* (7)	*xiii*

Legonea hyperiodriloides Clausen, 1963

Legonea hyperiodriloides Clausen, 1963, Vidensk. Medd. fra Dansk naturh. Foren., **126** : 2.–Legon, 10 miles N.E. of Accra, Ghana.

85 clitellate specimens, Nimghah Farm, Ahulu, 20th June, 1956.

Legonea modesta Sims, 1964

Legonea modesta Sims, 1964, Proc., zool. Soc. Lond., **143** : 595.–Ketekrachi, southeastern Ghana.

15 clitellate, 1 aclitellate specimens (syntypes), 14th February, 1951. 1 aclitellate specimen, Tafo, 14th May, 1954.

Legonea rapta Sims, 1964

Legonea rapta Sims, 1964, Proc. zool. Soc. Lond., **143** : 601.–Jangebunga, southeastern Ghana.

58 clitellate specimens (holotype and paratypes), 10th December, 1951.

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THE CICHLID FISHES OF LAKE NABUGABO, UGANDA

By P. H. GREENWOOD

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INTRODUCTION

LAKE NABUGABO is a small body of open water lying within an extensive swamp which fills a former bay on the western shore of Lake Victoria (see map, fig. 1.). Its shape is roughly pyriform, the main axis about five miles long and the width approximately three miles. Except for the western shore, the lake margin is swamp. The western shore is more varied, with, in some places, gently sloping sandy beaches and in other places forest reaching to the lake edge. The swamp margin begins with a zone of Hippo grass (*Vossia cuspidata*) whose rhizomes grow out into the open water. Behind the Hippo grass is a high "hedge" of the grass *Miscanthidium* forming a floating platform of matted roots and rhizomes jutting out into the lake. Away from the margin this platform becomes more solid through the addition and incorporation of dead and decaying vegetation. In places the platform, although still afloat, is sufficiently compacted to support the growth of trees.

Along its eastern and south-eastern lakeside boundaries the *Miscanthidium* zone is replaced by a large area of *Sphagnum* swamp, an unusual feature at this altitude in east Africa and one not encountered in the swamps around Lake Victoria.

The Bladder-wort *Utricularia* is common in the open water pools found within the eastern part of the swamp. In this region the dominant plant is the grass *Loudetia phragmitoides*, its tussocky habit allowing the development of small open pools. *Utricularia* is also common in the sheltered bays and inlets around the lake margin, and along the sheltered open shores.

Two species of water-lily (*Nymphaea lotus* and *N. caerulea*) occur in the open lake, especially in sheltered bays. Some stands of *Papyrus* are found all around the lake shore but this plant is nowhere a dominant. The relative scarcity of *Papyrus* in Nabugabo contrasts strongly with other swampy areas in the surrounding countryside and, particularly, in Lake Victoria (For a more detailed account, see Beadle and Lind, 1960).

Nowhere in Lake Nabugabo is the water more than fifteen feet deep; in most places it is between five and twelve feet. Except along the western shore the bottom does not shelve and it is in that area that the few patches of exposed sandy bottom are found. Elsewhere the sand is covered by a blanket of liquid mud (Cambridge expedition's field notes).

Very little published information is available on the hydrology of the lake. During the visit of the second Cambridge expedition (June to August, 1962) the open water was well-mixed and supersaturated with oxygen, even in the upper layers of mud. The oxygen content fell sharply in the deeper mud layers and in the water at the bottom of swamp inlets; surface water in these inlets was, however, as highly oxygenated as that of the open lake.

The water of Nabugabo is more alkaline than that of Lake Victoria (pH. of open water 8·2 *cf* 7·8 for Victoria) but in the surrounding swamps it is more acid (pH. 5·35–6·00). Perhaps the most striking hydrological feature is the very low salt concentration of the lake water; its electrical conductivity is about a quarter of that for water from Lake Victoria. Unfortunately no detailed water analyses are yet available.

The main affluents to Nabugabo are the Juma river and the Lwamunda swamp; the latter is fed by small, swampy rivers. Numerous small springs discharge along the western lake shore. The outflow of the lake is into Lake Victoria (some fifty feet lower) and is effected solely by seepage through the sand-bar which forms the eastern barrier between the two water masses; there is no surface contact.

Present day lake Nabugabo represents the greatly diminished body of open water which was gradually cut off from Lake Victoria by the formation of longshore bars across the mouth of an extensive open bay. Bishop (1959) has described the probable history of this empondment: "The landward shore of the lake was an old shoreline of Lake Victoria which consisted in the south-west of a lateritic oldland with low cliffs.

The Juma River divided the oldland into two spurs which were linked again by a series of bay bars across its mouth. Further to the north, a curving longshore bar protruded to the north-east from the mainland and finally joined a former island at Kisasa."

"At some later period another complex longshore bar commenced to grow towards the north-north-east from a point six miles south of the Juma River and finally it also reached the former island of Kisasa to complete the enclosure of Lake Nabugabo. The lake is at present approximately 50 feet above Lake Victoria and is rapidly being overgrown by swamp vegetation. The open water is now separated from the parent lake to the south-east by more than a mile of swamp and two miles of complex sand and gravel ridges comprising the longshore bar."

The age of Lake Nabugabo has been estimated at approximately 4,000 years. This figure is based on the radiocarbon dating of some rolled charcoal fragments found in a former shoreline of Lake Victoria at about the same height above the present level of the lake as is the sandbar which cuts off Nabugabo (personal communication from Dr. Bishop quoted by Beadle, 1962).

The first collections of fishes from Lake Nabugabo were made in 1930 by the

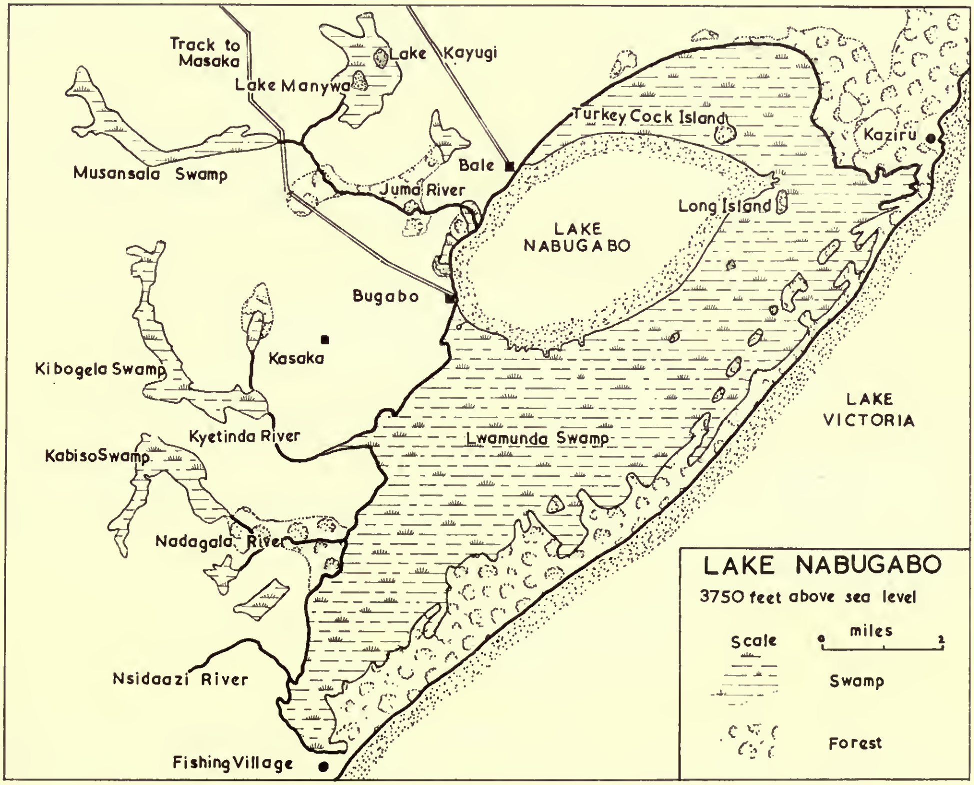
Track to Masaka
Lake Kayugi
Lake Manywa
Musansala Swamp
Turkey Cock Island
Kaziru
Bale
Juma River
Long Island
LAKE NABUGABO
Bugabo
Kasaka
Kibogela Swamp
Kyetinda River
Kabiso Swamp
Lwamunda Swamp
LAKE VICTORIA
Nadagala River
Nsidaazi River
Fishing Village
LAKE NABUGABO
3750 feet above sea level
Scale
miles
0
2
Swamp
Forest

FIG. 1. Sketch map of Lake Nabugabo; after a map produced by the Cambridge Nabugabo Biological Survey.

Cambridge expedition to the East African Lakes. The Cichlidae were studied by Dr. Ethelwynn Trewavas (1933) who recognised their importance in helping to understand the evolutionary processes which had resulted in the complex *Haplochromis* species-flock of Lake Victoria. Dr. Trewavas recorded four *Haplochromis* species, of which three were described as new and endemic, and the fourth assigned to a species already known from Lake Victoria.

Since 1930 our knowledge of Lake Victoria *Haplochromis* has increased, both from the systematic and from the ecological view-points. So too has our knowledge about the geological history of the area, and there has recently been revived interest in the evolutionary problems posed by the cichlid species-flocks. Thus, it seemed desirable to revise the *Haplochromis* of Lake Nabugabo against the newly acquired information from Lake Victoria. This possibility became a reality when a group of Cambridge students offered to collect specimens from Lake Nabugabo for the British Museum (Natural History). Their collection (hereinafter referred to as the C.N.B.S. collection) has proved invaluable for several reasons. Not only did it substantially increase the number of specimens but the expedition also made detailed notes on the live colours of the fishes, and on their distribution and habitats. Observations were also made on the fishes' feeding habits and some data on breeding conditions were collected as well. With this sort of information it was possible to make a more detailed and direct comparison between the *Haplochromis* of the two lakes and thus to make a reappraisal of relationships on characters other than purely anatomical ones.

To the original four *Haplochromis* species must now be added two others and two species of *Haplochromis*-group genera, *viz. Hemihaplochromis multicolor* (Schoeller) and *Astatoreochromis alluaudi* Pellegrin. Three of the newly recorded species (*H. nubilus, Hh. multicolor* and *A. alluaudi*) are of fairly wide distribution in the Lake Edward-Victoria drainage basins; their occurrence in Lake Nabugabo is not surprising. Unfortunately it is not absolutely certain that one can accept their presence as natural because some introductions have been made into Lake Nabugabo since the original collections were made over thirty years ago. In 1960, the Nile Perch (*Lates*) was introduced. If the newly recorded cichlids gained access in this way it was accidental and, I would consider, unlikely if only Nile Perch were involved. *Haplochromis* are more likely to be introduced accidentally when *Tilapia* are moved from one area to another because small individuals of the two genera are easily confused.

In addition to the cichlid fishes described below, the C.N.B.S. collection contained a large number of non-cichlid species, including several new records for the lake. These fishes will be dealt with in a separate publication.

THE FISHES

I. ***TILAPIA*** A. Smith, 1840

Two species of *Tilapia* (*T. esculenta* Graham and *T. variabilis* Blgr.) are recorded from Lake Nabugabo; both are otherwise endemic to Lakes Victoria and Kyoga. The C.N.B.S. mentioned both species in their preliminary report but no specimens were sent to the British Museum (Nat. Hist.).

II. ***HAPLOCHROMIS*** Hilgendorf, 1888

Regan, C. T. 1920. The classification of the fishes of the family Cichlidae. I. The Tanganyika genera. *Ann. Mag. nat. Hist.* (9), **5** : 33–53.

Haplochromis velifer Trewavas, 1933

(Text figs. 2 and 3)

H. velifer (part) Trewavas, 1933, *J. Linn. Soc.* (*Zool*), **38** : 322.

HOLOTYPE. A male 75 mm. S.L., B.M. (N.H.) Reg. No. 1933.2.23.194, collected by E. B. Worthington.

DESCRIPTION. Based on the holotype, 6 paratypes and eight additional specimens, 75–108 mm. S.L.

Depth of body 35·7–41·3 (Mean, M, = 39·1) per cent of standard length, length of head 32·3–36·0 (M = 34·7) per cent; dorsal profile of head slightly curved (but with a concavity above the orbit), sloping moderately steeply (*ca* 40°–45° to the horizontal).

Preorbital depth 13·8–18·5 (M = 16·3) per cent of head length, least interorbital width 21·8–29·0 (M = 24·1) per cent and snout length 29·1–33·4 (M = 31·3); snout slightly broader than long or as long as broad. Eye diameter shows weak negative allometry with standard length, 26·3–33·4 (M = 30·6) per cent of head; depth of cheek 21·8–26·0 (M = 23·3) per cent.

Caudal peduncle 14·5–17·5 (M = 15·9) per cent of standard length, 1·2–1·4 (mode 1·3) times as long as deep.

Mouth horizontal or very slightly oblique; jaws equal anteriorly, the lower 37·1–44·8 (M = 39·7) per cent of head, 1·4–2·0 (mode 1·5) times as long as broad. Lips often slightly thickened. Posterior tip of the maxilla reaching (the modal

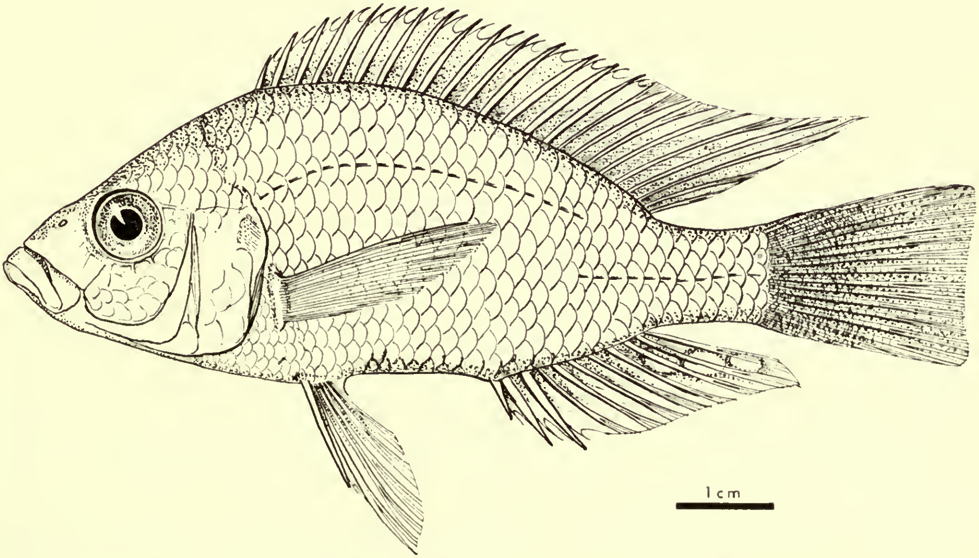

FIG. 2. *Haplochromis velifer*. Drawn by Barbara Williams.

condition) or almost reaching the vertical through the anterior orbital margin but in four specimens extending to below the anterior part of the eye.

Gillrakers short and stout, 7–9 (mode 8) on the lower limb of the first arch, the lowermost one to three rakers reduced.

Scales ctenoid; lateral line with 30 (f.4), 31 (f.7) or 32 (f.4) scales; cheek with 3 (f.14) or 4 (f.1) rows; 5–6½ (mode 6) scales between the dorsal fin origin and the upper lateral line, 5–6 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.10) or 25 (f.3) rays comprising 15 (f.11) or 16 (f.3) spinous and 8 (f.3), 9 (f.9) or 10 (f.2) branched elements; anal with 11 (f.5) or 12 (f.9) rays comprising 3 spinous and 8 (f.5) or 9 (f.9) branched rays. Caudal fin truncate or subtruncate with slightly rounded distal corners (Trewavas, *op. cit.*, suggests that the degree of rounding is greatest in males), scaled on its basal half. First two branched pelvic rays produced in both sexes. Pectoral 25·4–29·8 (M = 27·6) per cent of standard length.

Teeth. The outer teeth in both jaws are slightly recurved, relatively stout and have compressed bicuspid crowns (see text-fig. 3); the postero-lateral and posterior teeth are somewhat less robust than those situated anteriorly. The acutely pointed smaller cusp is prominent and stout; the major cusp has an oblique edge which meets the nearly vertical medial aspect of the cusp at an angle of 45°–60°. There are 40–58 (mean 50) teeth in the outer row of the upper jaw.

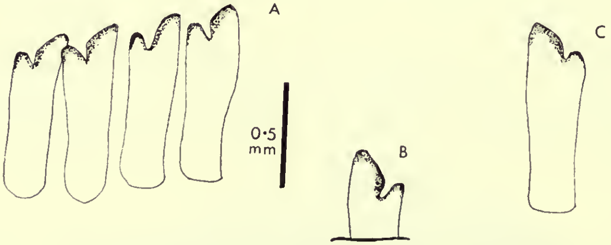

FIG. 3. *Haplochromis velifer.* Outer teeth (labial aspect) from: A, premaxilla, and C, dentary. B, newly erupted tooth (dentary).

The inner rows in both jaws are composed of small, compressed and tricuspid teeth arranged in 2–4 (mode 3) and 2 (mode) or 3 rows in the upper and lower jaws respectively. A distinct interspace separates the inner rows from the outer row.

The form of the outer teeth in *H. velifer* is one of the two generalized types found in many species of *Haplochromis*. In the other type, the major cusp is more acutely pointed.

Lower pharyngeal bone slender, the triangular dentigerous surface broader than long. The teeth are slender and cuspidate, fairly close-set and arranged in 24–28 antero-posterior rows; teeth in the two median rows are generally somewhat stouter than the others but are otherwise identical.

Vertebrae: 28 or 29, comprising 13 abdominal and 15 (f.2) or 16 (f.7) caudal elements.

Coloration in life. Males (adult but of undeterminable sexual state): ground colour dark grey-blue to olivaceous dorsally (dark indigo on head), shading on flanks to olivaceous with violet to turquoise sheen; ventral surface sooty-violet, the chest with a red flush. Males less than 65 mm. S.L. and probably juvenile have a similar coloration dorsally and laterally but the ventral surface is silvery-white and the chest lacks the red flush.

Dorsal fin dark olive (overlain with sooty in fishes >65 mm. S.L.) basally, light blue-grey distally; dull red spots and blotches between the rays; the lappets and margin to the soft part crimson. Anal fin greenish-blue basally, buff to pink distally (olivaceous in small fishes); ocelli orange with light yellow surround on a transparent area of fin membrane. Pelvics with anterior quarter sooty except for the dead-white, elongated first and second rays; remainder of fin hyaline in fishes <65 mm. S.L., pink to crimson in larger individuals. Caudal fin dark olivaceous to indigo proximally, light olive distally in small fishes, scarlet in larger ones.

Females: ground colour dull metallic grey with violet lights (particularly on the cheeks), shading through greyish-buff on the flanks to pinkish-white on the ventral surface.

Dorsal fin pale buff with a narrow basal band of crimson on that part of the fin posterior to the fifth spine. Anal with a crimson basal band followed by a broader buff band and, along the distal margin, a narrow sooty band; in some specimens there are dull orange spots in about the position of the ocelli in males. Pelvics faintly sooty.

Coloration in preserved specimens. Adult males. Body dark brown, black on belly and chest, in ripe individuals this dark coloration extending along the entire ventral surface and on the flanks as far dorsally as the upper lateral line; in some specimens there is a pearly sheen visible on the dark areas. A well-developed lachrymal stripe of varying width, two parallel transverse bars on the snout and two transverse nuchal bands are also present. The anterior nuchal band is a continuation of the lachrymal stripe; the posterior band originates at the anterior, upper angle of the operculum and also extends ventrally along the preopercular-opercular junction. On the flanks there are traces of six, moderately broad bands which reach the origin of the dorsal fin and fuse ventrally with the dark belly; these bands are much fainter than the nuchal and snout bars.

The dorsal fin in sexually quiescent fishes is hyaline but in active individuals it has dusky lappets and a solid, parabolic dusky area originating at the base of the third to sixth spinous ray from where it rises fairly steeply so that the area of membrane between the 10th and last spine is completely black; thereafter it falls rather gently so that the distal third to half of the membrane between the branched rays is hyaline but the base is black. Caudal fin is hyaline in quiescent fishes but the proximal two-thirds is black in active individuals; in some specimens darker spots are visible through the sooty ground colour. The anal has the entire interspinous membrane black; in active fishes the basal third to half of the soft part is black, the remainder hyaline (as is the entire fin in quiescent individuals); two or three, dead-white, round to oval ocelli are present in both sexes.

Certain variant patterns are fairly common; the most frequently seen being variation in the intensity and area of the dark parabola of the dorsal fin and a tendency for the posterior nuchal bar to be expanded medially into a large triangular black patch with its apex at the base of the first dorsal spine.

Females are greyish-silver, darkest dorsally; there is a fairly distinct lachrymal stripe running from the angle of the jaw through the anterior rim of the orbit. All fins are hyaline, with the soft dorsal and caudal maculate, and dark lappets to the dorsal in some specimens. Traces of six narrow vertical bars may be visible on the flanks; these do not extend to the belly and they become extremely faint near the base of the dorsal fin.

Ecology. Habitat. Haplochromis velifer has a wide distribution within the lake, being found both close inshore and at some distance out, over muddy and sandy bottoms in bays, and over the clear sandy beaches of the western shore. It does not appear to live in the isolated swamp pools, nor does it extend far up those arms of the lake which penetrate into the swamps.

Food. The C.N.B.S. notes, supplemented by a personal examination of eight additional specimens, indicate that *H. velifer* is an omnivorous bottom feeder with insect larvae (especially those of chironomids and trichopterans) providing the main source of nourishment. A considerable amount of plant material was found in the gut but it showed few signs of digestion. Since the bottom in many habitats is covered by a layer of plant matter (both algal and phanerogamic) the plant remains should probably be considered as being incidentally ingested during the search for insect larvae and other invertebrate animals. Sand grains were also recorded and in some instances these could be identified as coming from the cases of larval Trichoptera.

Breeding. No data are available. The largest specimen (108 mm. S.L.) is a female, but both sexes are found in the next largest size group, 75–85 mm. S.L.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. Anatomically and trophically *H. velifer* belongs to the group of generalized *Haplochromis* which are found both in the rivers and in the species-flocks of the major lakes. Comparison will be made first with the widely distributed species *H. nubilus* and *H. wingatii*, the former occurring in Lakes Nabugabo, Victoria and Edward, the latter in Lakes Edward and Albert and in the Nile.

From *H. velifer*, *H. nubilus* is immediately distinguished by the velvety black and uniform body colour of adult males, as well as by its stouter and more acutely cuspidate teeth, more obviously rounded caudal fin and its smaller eye. *Haplochromis wingatii* differs in having fewer teeth in the outer row of the upper jaw (30–40 in specimens of a size comparable with the *H. velifer* sample examined), larger and more numerous unicuspid teeth posterolaterally in this row, markedly smaller scales on the chest region, in having some blunt pharyngeal teeth and in the coloration of adult males.

Amonst the Lake Victoria endemics, *H. velifer* is perhaps nearest to *H. cinereus*, *H. macrops*, *H. lacrimosus* and *H. pallidus*. It differs from all these species in various combinations of characters (see Greenwood, 1960). In all cases the nature of the preserved coloration serves to separate males of the various species; the live coloration of male *H. macrops* (the only species of the four in which this is known) also differs markedly from that of *H. velifer*. The most obvious anatomical characters distinguishing *H. velifer* from the Victoria species are: from *H. cinereus* the dentition (in *H. cinereus* slender unicuspid or weakly bicuspid outer teeth, uni- and bicuspid, obliquely implanted inner teeth); from *H. macrops*, the absence of tricuspid teeth posterolaterally in the upper, outer tooth row of fishes <85 mm. S.L., smaller eye (26·3–33·4, M = 30·6% of head in *H. velifer, cf.* 28·6–35·4, M = 33·0 in *H. macrops*) and deeper cheek (21·8–26·0, M = 23·3% of head *cf.* 17·4–24·2, M = 21·1 in *H. macrops*); from *H. lacrimosus*, the more robust less curved outer teeth with their expanded major crowns, the shorter pectoral fin (M = 81% of head in *H. velifer*, 88·5% in *H. lacrimosus*) and slightly deeper cheek (21·8–26·0, M = 23·3% of head, *cf.* 17·6–23·5, M = 20·5% in *H. lacrimosus*); from *H. pallidus* (which species *H. velifer* closely resembles in its oral dentition) the larger chest and nape scales, the fewer teeth in the median tooth row of the lower pharyngeal bone, and a lower modal number of gillrakers (8 cf. 9 for *H. pallidus;* the range of gillraker numbers (7–9) is identical).

In her original description of *H. velifer*, Trewavas (1933) compared the species with *H. gestri* (now a synonym of *H. obesus* (Blgr), see Greenwood 1959b). The two species are but distantly related, *H. obesus* belonging to the group of specialized larval-fish eating species which is characterized by a reduced dentition and an expansible mouth.

Amongst the Lake Edward endemics *H. velifer* shows the greatest superficial resemblance to *H. schubotzi*. It differs from this species in the following characters: its dentition, a shallower preorbital, and a shorter caudal peduncle. Small specimens of *H. schubotzi* (i.e. in the range comparable with that known for *H. velifer*) have relatively slender teeth with the minor cusp reduced and the major cusp acutely pointed; in larger specimens the teeth are, relatively, even more slender and may have the minor cusp reduced almost to vanishing point. In specimens at all sizes the inner teeth of *H. schubotzi* are tricuspid, but in specimens over 120 mm. S.L. the cuspidation is feebly manifested. Trewavas (1933), believed that the lower jaw of *H. schubotzi* is longer than in *H. velifer* but I am unable to confirm this; the lower jaw has the same relative length in both species.

The other Lake Edward species showing a superficial resemblance to *H. velifer* are *H. nigripinnis*, *H. eduardii* (including *H. vicarius* acc. Poll, 1939), *H. elegans* and *H. engystoma*.

Both *H. nigripinnis* and *H. engystoma* are distinguished from *H. velifer* by their shorter snouts, larger eyes (eye diameter about equalling snout length in *H. velifer*, much longer than snout in the two Edward species), more decurved dorsal head profile and, in *H. nigripinnis*, by the more slender and numerous gill rakers (10 or 11); also, *H. engystoma* has fewer teeth (36 in the upper, outer row of the unique holotype) with more strongly recurved cusps.

From *H. eduardii*, *H. velifer* is distinguished by its coarser teeth (and the absence of unicuspids in larger specimens), shorter, coarser and fewer gill rakers (7–9, *cf.*

9–12 in. *H. eduardii*), straighter dorsal head profile and shorter pectoral fin (always clearly shorter than the head in *H. velifer*, as long as the head, or nearly so, in *H. eduardii*).

Haplochromis elegans differs least of all but is nevertheless distinguished by its shallower body, somewhat shorter snout, smaller chest scales (both ventrally and laterally) and its more strongly curved dorsal head profile.

Haplochromis velifer certainly appears to have greater affinity with the Lake Victoria species discussed here than with those of Lake Edward. *Haplochromis elegans* is the only Edward species to have about the same overall degree of affinity with *H. velifer* as have the Victoria species. However, it must be remembered that these comparisons are based on fewer Edward than Victoria specimens and that less is known about their ecology and live colours.

Within Lake Nabugabo, *H. velifer* has closest affinity with the new species, *H. simpsoni* (see p.325); indeed, five paratypes of *H. velifer* are now identified as *H. simpsoni*. The species are distinguished principally by their dentition; the outer teeth of *H. simpsoni* are more slender, have an acutely pointed major cusp (the minor cusp greatly reduced or absent) and are more numerous (50–70, mean 60, in the outer, upper series, *cf.* 40–58, M = 50, for *H. velifer*). The body form of the two species is similar although the dorsal head profile of *H. simpsoni* is straighter and lacks the interorbital concavity of *H. velifer;* also, in *H. velifer* the orbit lies distinctly below the outline of the profile, whereas in *H. simpsoni* the upper margin of the orbit is generally included in the profile. In *H. velifer* the snout is broader than it is long (or at least as broad as long) but in *H. simpsoni* the snout is longer than broad (the difference becoming more pronounced in larger fishes) so that these fishes have the appearance of being thinner faced than *H. velifer*. This is reflected in the width of the lower jaw; the mean length/width ratio for *H. velifer* is 1·5 (range 1·4–1·7) and for *H. simpsoni* 2·0 (range 1·5–2·1). A difference also exists in the modal number of gill rakers (7 for *H. simpsoni*, 8 for *H. velifer*) and the lower limit for *H. velifer* is higher (7 *cf.* 6 for *H. simpsoni*). Finally, there are differences in the coloration of adult males; *H. velifer* has a red flush on the chest and crimson lappets to the spinous dorsal, this colour continuing onto the margin of the soft dorsal as well. In *H. simpsoni* the chest is sooty and the dorsal lappets black. There are also interspecific differences in the colours of the anal, caudal and pelvic fins, and the body is more definitely blue in *H. simpsoni*.

No single anatomical character can be considered diagnostic but if those mentioned above are taken in concert, the two species may be distinguished fairly readily.

Study material

B.M. (N.H.) reg. no.	*Collector*
1933.2.23.194 (Holotype)	Worthington
1933.2.23.181–193 (Paratypes) . . .	Worthington
1933.2.23.200–209	Worthington
1964.7.1.34–50	C.N.B.S.

Haplochromis simpsoni sp. nov.

(Text figs. 4 and 5)

H. velifer (part) Trewavas, 1933, *J. Linn. Soc. Soc.* (*Zool.*), **38** : 322. (See list of study material.)

HOLOTYPE. An adult male 88 mm. standard length (B.M.[N.H.] reg. no. 1964.7.1.12) collected by the C.N.B.S.

Named in honour of Mr. M. Simpson, one of the members of the Cambridge Nabugabo Biological Survey.

DESCRIPTION. Based on the holotype and twenty-one additional specimens, 76–114 mm. S.L.; data on dentition were also derived from eighty further specimens, collected by Capt. C. R. S. Pitman.

Depth of body 32·7–42·0 (M = 37·6) per cent of standard length, length of head 31·6–37·6 (M = 34·9) per cent. Dorsal profile of head straight (without a noticeable concavity above the eye), sloping at about 45° to the horizontal.

Preorbital depth 16·1–20·5 (M = 17·8) per cent of head, least interorbital width 18·8–24·7 (M = 22·3) per cent, length of snout 28·8–34·3 (M = 32·2) per cent; snout longer than broad. Eye diameter 25·6–32·4 (M = 29·4) per cent of head (not showing any allometry in the sample studied), depth of cheek 22·4–28·2 (M = 25·0) per cent.

Caudal peduncle 15·3–18·5 (M = 16·7) per cent of standard length, 1·1–1·6 (mode 1·4) times as long as deep.

Mouth horizontal (rarely, slightly oblique); jaws equal anteriorly, the lower 37·5–45·0 (M = 41·4) per cent of head, 1·5–2·1 (mode 2·0) times as long as broad. Posterior tip of maxilla reaching or almost reaching the vertical through the anterior orbital margin or even to slightly beyond this point.

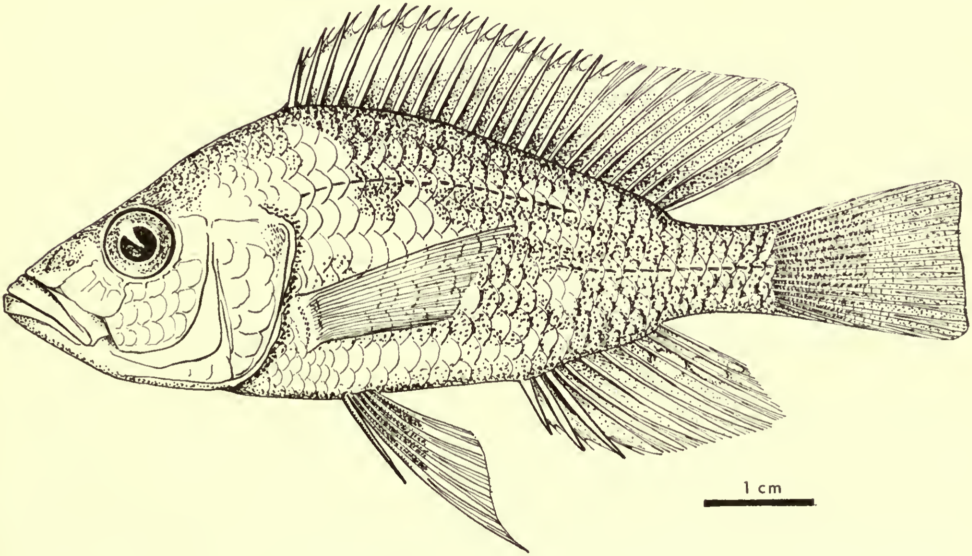

FIG. 4. *Haplochromis simpsoni.* Drawn by Barbara Williams.

Gillrakers variable, from stout to moderately slender, both extremes often occurring on the same arch; 6–9 (mode 7) on the lower part of the first arch, the lowermost 1 to 3 rakers reduced.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.2), 32 (f.10) or 33 (f.8) scales; cheek with 3 (f.13) or 4 (f.9) rows; 5–7 (modal range 5½–6) scales between the upper lateral line and the dorsal fin origin; 5 or 6 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.8) or 25 (f.14) rays, comprising 15 (f.8) or 16 (f.14) spinous and 8 (f.1), 9 (f.20) or 10 (f.1) branched rays. Anal with 11 (f.12) or 12 (f.10) rays, comprising 3 spinous and 8 (f.12) or 9 (f.10) branched rays. Pectoral 26·4–33·2 (M = 27·6) per cent of standard length. First and second pelvic rays produced, proportionately more so in adult males. Caudal subtruncate.

Teeth. There are three forms of teeth in the outer row of both jaws; all are slender and recurved, and all have an acutely pointed major cusp. The commonest form has a very weakly developed minor cusp which appears as little more than a lateral spur at the base of the protracted, slender and curved major cusp (text fig. 5); a variant of this type lacks the minor cusp, either through wear or because the tooth develops without it (as can be determined from erupting teeth). The third form is relatively stouter than the other two types, has a small but distinct minor cusp and a less protracted and less acutely pointed major cusp; this form is usually restricted to a posterolateral position in the row. An admixture of all forms of tooth may occur in any fish and usually there is no difference in the proportion of the two commoner types as between upper and lower jaws. However, in some individuals the unicuspids occur in the upper jaw and the weakly cuspidate form in the lower (where there may also be a few of the stouter, more definitely bicuspid teeth). No obvious correlation exists between the sex or size of the fish and the type of dentition present.

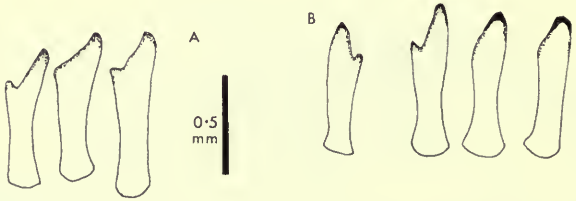

FIG. 5. *Haplochromis simpsoni.* Outer teeth (labial aspect) from: A, dentary, and B, premaxilla.

There are 50–70 (mean 60) teeth in the outer row of the upper jaw; the tooth number has a weak positive correlation with the size of the specimen.

The inner rows (2 [mode] or 3 in the upper jaw and 1–3 [mode 2] in the lower) are also made up of three different types of teeth. A tricuspid tooth with a protracted middle cusp is the commonest form, but weakly bicuspids and even unicuspids also occur, although much less frequently and in fewer numbers.

In many specimens the teeth are coarsely disfigured by a dark brown thickening of the crown which, in many cases, almost obscures the nature of the cusp. A similar (? pathological) condition was found in *H. empodisma* of Lake Victoria (Greenwood, 1960), a species thought to be related to *H. simpsoni;* it is also seen in the very distantly related *H. obliquidens* of Lake Victoria (Greenwood, 1956).

Lower pharyngeal bone slender; its dentigerous surface triangular and slightly longer than broad. The pharyngeal teeth are slender and cuspidate, and are arranged in 26–28 rows; the median rows may contain a number of somewhat coarser teeth but in the majority of specimens examined no such differentiation was apparent.

Vertebrae: 29, comprising 12 (f.1) or 13 (f.8) abdominal and 16 (f.8) or 17 (f.1) caudal elements.

Coloration in life. Adult males: dorsal surface of body cobalt, that of the head dark umber to black; flanks with light turquoise sheen, the ventral body surface sooty except for the chest which is silvery-white with a diffuse sooty overlay.

Dorsal fin pale grey with small blotches of dull red between the spines, and darker, more irregular red blotches between the branched rays; lappets and margin to soft part black. Caudal fin dark turquoise on its proximal half, followed by a broad, pinkish vertical band and, distally, a blackish area extending to the margin; the posterior angles are sometimes outlined in red. Anal greyish-white, lappets sooty; a faint pink flush extends along the distal margin of the soft part and spreads, but less definitely, to below the black lappets of the spinous portion. Pelvics olivaceous with a sooty wash.

Females: body olive-green, with a suggestion of blue dorsally, becoming lighter on the flanks (which have a turquoise iridescence) and shading to blue-grey ventrally. Cheek and opercular region with turquoise high-lights.

Dorsal fin olive-green basally, the posterior part lightest; dull red blotches occur between the spines and give an impression of a broad red stripe along this part of the fin and even to the more distal region below the black lappets. Similar but smaller blotches occur between the soft rays so that the band is continued posteriorly where, however, it is narrower and less intense. Caudal fin with a reddish to olive-brown blotch at its base, the blotch becoming brighter red distally; the area around the blotch is olive-yellow as is the middle third of the fin; the distal third is either sooty or olive-yellow. Anal fin olive-yellow except for a dull crimson basal streak. Pelvics pale olive-yellow, the elongated rays dead white.

Coloration in preserved specimens. Adult males (*sexually active*) are light brown, with the belly, isthmus, flanks (to the level of the upper lateral line) and caudal peduncle (except dorsomedially) sooty to black; the cheeks are dark but with a pearly lustre. Two narrow transverse bars are usually visible across the snout but apparently only one nuchal band is developed; the latter originates at the anterior upper angle of the operculum and is usually interrupted medially. The lower jaw is pale but the branchiostegal membrane is black. The dorsal fin is hyaline with a sooty overlay most concentrated in the middle third of the fin and least concentrated on the distal region of the soft part. Caudal fin is dark on its proximal quarter, lighter over the remainder except along a moderately wide band outlining its ventral and posterior margins. The anal fin is faintly white to hyaline except for a narrow, intensely dark basal streak and four greyish ocelli (arranged in a single row). The pelvics are black to sooty, being lightest on the posterior third.

Sexually quiescent males are light brown, the chest, belly, branchiostegal membrane and the lower half of the caudal peduncle dusky and overlaid with a pearly sheen; the two snout- and single nuchal-bands are as in active males. Five or six vertical bars of variable intensity are visible on the flanks; these do not reach the origin of the dorsal fin and ventrally they merge with the dark ventral coloration. Dorsal fin hyaline with dark lappets, caudal dark hyaline, darkest proximally; anal dusky, darkest (almost black) in the area of the spines, two to four greyish ocelli arranged in one or two rows. Pelvic fins black to sooty.

Females are silvery-grey; a short, broad lachrymal stripe or blotch is present, as are a faint nuchal bar and an even fainter transverse bar across the snout. Six or seven faint but moderately broad bars are visible on the flanks and caudal peduncle, those on the flanks reaching neither the dorsal nor ventral body outlines. All fins are hyaline, the base of the caudal slightly darker; in one specimen there is a faint darkening between the rays of the dorsal fin (especially over the soft part) and over the proximal two-thirds of the caudal fin. In all specimens there are two dark spots on the anal in the position of the ocelli in males.

Ecology. Habitat. This species seems to have a wide distribution within the lake, being found inshore over a variety of substrata, amongst the emergent vegetation, over exposed sandy beaches and even at some distance offshore over a muddy bottom. It does not appear to inhabit isolated pools in the swamps, nor does it extend for any distance up the inlets into the swamps. Thus, it will be seen that *H. simpsoni* and *H. velifer* do not differ in their broad ecological requirements or restrictions.

Food. From the C.N.B.S. field notes, supplemented by further gut analyses on five specimens, I can find no clear-cut differences in the feeding habits of this species and *H. velifer* (see p. 322); that is, *H. simpsoni* is an omnivorous bottom feeder preying chiefly on insect larvae.

Breeding. No data are available. All the specimens examined are adult, the smallest male and female being 76 and 85 mm. S.L. respectively. The largest fish is a female (114 mm. S.L.) and the largest male is 105 mm. S.L.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. The nature of the dentition, together with the relative size of the eye and snout, serves to distinguish *H. simpsoni* from the generalized species of Lake Edward (i.e. *H. eduardii*, *H. engystoma*, *H. nigripinnis*, *H. elegans* and *H. schubotzi*). On the basis of its dentition, *H. simpsoni* cannot be included in the same category as these generalized species (although trophically it should be considered generalized). Rather, it should be grouped with *H. empodisma* of Lake Victoria, a species with which it shows fairly close affinities.

The body form and, particularly, the dentition of *H. empodisma* and *H. simpsoni* are similar as are the feeding habits and broad ecological requirements of the two species (Greenwood, 1960). *Haplochromis simpsoni* is, anatomically, more closely related to *H. empodisma* than it is to the small, undescribed, species which I mentioned in connection with the affinities of *H. empodisma* (see Greenwood, *op. cit.*). *Haplochromis simpsoni* differs from *H. empodisma* in having somewhat fewer jaw teeth (50–70, M = 60 *cf.* 54–82, M = 70), the triangular dentigerous surface of the lower pharyngeal bone equilateral and not isoscelean, a slightly narrower head (15·0–16·7, M = 15·9 per cent of standard length, *cf.* 15·6–19·8, M = 17·4 per cent in *H. empodisma*) and a straighter dorsal head profile. The modal number of dorsal rays in *H. empodisma* (24) is lower than in *H. simpsoni* (25) although the ranges overlap; however, the range in *H. empodisma* includes a number of specimens with only 23 rays and but one fish with 25. The two species differ in the coloration of adult males, especially in the absence of red pigment on the head of *H. simpsoni*; the red head of *H. empodisma* is a characteristic feature.

Haplochromis simpsoni also resembles *H. velifer*; the diagnostic characters separating these species are discussed on page 324. In sum, it seems that *H. simpsoni* shares more characters with *H. empodisma* than with *H. velifer*.

STUDY MATERIAL

B.M. (*N.H.*) *reg. no.*	*Collector*
1964.7.1.12 (Holotype)	C.N.B.S.
1964.7.1.13–24 (Paratypes)	C.N.B.S.
1964.7.1.25–27 (Paratypes)	Pitman
1933.2.23.195–199 (Paratypes of *H. velifer*) Paratypes	Worthington
1964.7.1.28–33 (Paratypes)	Pitman
1935.8.23.34–63	Pitman
1935.8.23.81–100	Pitman

Haplochromis annectidens Trewavas, 1933

(Text figs. 6 and 7)

H. annectidens (part) Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 323.

HOLOTYPE. An adult male, 67 mm. S.L. from Lake Nabugabo (collected by E. B. Worthington), B.M. (N.H.) reg. no. 1933.2.23.210.

DESCRIPTION: based on the holotype, seven paratypes and thirteen additional specimens, 43–67 mm. S.L.

Depth of body 31·3–40·0 (M = 36·9) per cent of standard length, length of head 30·6–36·0 (M = 33·8) per cent. Dorsal profile of head straight, sloping moderately steeply (*ca* 40°–45° with the horizontal).

Preorbital depth 11·1–15·8 (M = 13·5) per cent of head, least interorbital width 21·0–29·2 (M = 25·3), snout length 25·0–31·6 (M = 27·9), eye diameter 30·4–37·5 (M = 33·3) and depth of cheek 12·5–21·7 (M = 18·1) per cent, the latter character showing slight positive allometry with standard length.

Caudal peduncle 14·7–18·6 (M = 16·3) per cent of standard length, 1·1–1·6 (mode 1·4) times as long as deep.

Mouth horizontal, lips sometimes slightly thickened. Jaws equal anteriorly, the lower 31·3–42·2 (M = 37·4) per cent of head length, 1·5–2·0 (modal range 1·5–1·6) times as long as broad; posterior tip of the maxilla reaching the vertical through the anterior orbital margin (the modal condition) or to below the anterior part of the eye.

Gillrakers variable, from short and stout to relatively slender, but usually of uniform shape in any one individual; 8–10 (mode 9) on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.6), 32 (f.12) or 33 (f.1) scales; cheek with 2 or 3 (mode) rows; 5–6 (mode) scales between the dorsal origin and the upper lateral line, 4–5½ (mode 5) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.2), 24 (f.8), 25 (f.10) or 26 (f.1) rays, comprising 15 (f.8) or 16 (f.13) spinous and 8 (f.5), 9 (f.14) or 10 (f.2) branched rays. Anal with 11 (f.2), 12 (f.17) or 13 (f.2) rays, comprising 3 spinous and 8 (f.2), 9 (f.17) or 10 (f.2) branched. Caudal subtruncate or truncate. Pectoral 25·4–30·8 (M = 27·6) per cent of standard length. First two soft pelvic rays produced, proportionately more so in males.

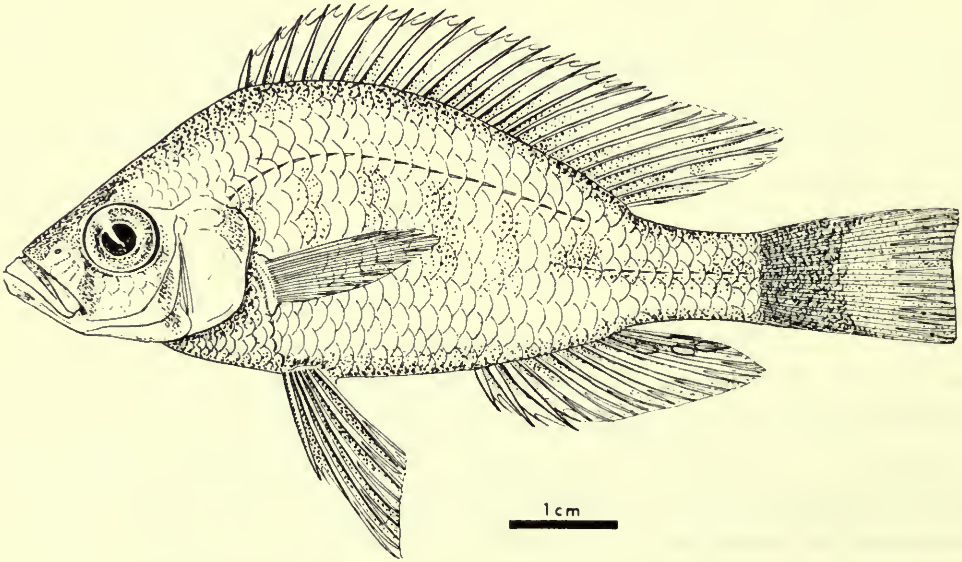

FIG. 6. *Haplochromis annectidens.* Drawn by Barbara Williams.

Teeth. The outer teeth in this species are highly characteristic. Except for a few teeth situated posteriorly in each jaw, the teeth are moveably implanted; each tooth has an elongate, slender neck and base but a flattened and expanded crown which is derived almost entirely from the enlarged major cusp (see fig. 7a, b). The occlusal margin of this cusp is obliquely truncate so that the thin occlusal surface is slightly convex and almost horizontal in position; the minor cusp is minute and acutely pointed. The anterior tip of the crown is drawn out, so that this margin of the tooth is concave; the posterior margin is curved in parallel with the anterior one (*i.e.* it is convexly arched). A few posterior teeth in the upper jaw are much smaller than their anterior congeners and are but weak replicas of them; in the dentary, the posterior teeth are tricuspid. The number of teeth in the outer, upper row shows some positive correlation with the size of the fish, *viz.* in fishes 43–50 mm. S.L. (N = 6), 38–50 (M = 45) and 48–68 (M = 56) in larger specimens (N = 15).

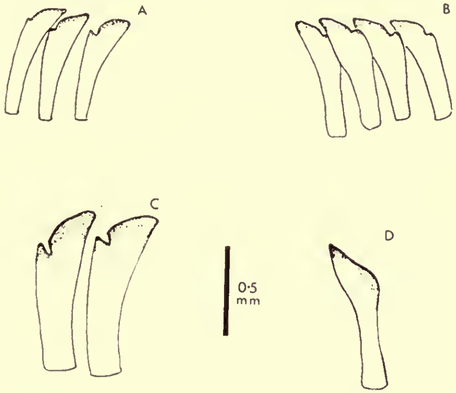

Fig. 7. A and B: *Haplochromis annectidens*, outer teeth (labial view) from, respectively, the premaxilla and the dentary. C, outer premaxillary teeth of *H. lividus* (labial view), D, outer tooth (premaxilla) in labial view, of *H. obliquidens*.

All teeth in the inner rows are small and tricuspid; in a few specimens the teeth of the outermost row may be noticeably enlarged but are still clearly tricuspid, unlike the enlarged inner teeth of *H. obliquidens* (see below p. 334) which are also obliquely cuspidate. There are 2–4 (mode) inner rows of teeth in the upper jaw and 2–4 (mode 3) in the lower; a fairly distinct interspace usually separates the inner rows from the outer row, but in some specimens it is obscured.

Lower pharyngeal bone and teeth. The lower pharyngeal bone is slender, its dentigerous surface triangular and somewhat broader than long (occasionally equilateral). The teeth are slender, weakly cuspidate, slightly curved and fairly close set in 30–36 rows. In the largest specimen examined (the holotype) a few of the posterior teeth in the median rows are slightly enlarged; in all other specimens there is no such differentiation.

Vertebrae: 28 or 29, comprising 13 abdominal and 15 (f.1) or 16 (f.5) caudal elements.

Coloration in life. The C.N.B.S. field notes on this species are extensive and cover a number of different sexual and emotional states. Overall coloration of *adult males* shows considerable variation both in intensity and in the extent of any one pigment, and is apparently correlated with the emotional state of the fish. However, the predominance of pink and red in fin coloration, irrespective of these factors, is an obvious feature, as is the amount of red on the flanks in sexually active individuals.

Quiescent males are light blue-grey above the lateral line; the flanks are orange-buff shading to light green on the ventral body surface and the lower half of the caudal peduncle. Traces of five indigo bars are visible on the mid-flank region but do not extend to the body outline. Dorsal surface of the head dark olive to reddish, cheeks and operculum greenish-yellow, sometimes with faint red blotches at the angles of the preoperculum and operculum. Lachrymal, trans-snout and nuchal stripes (see notes on preserved colours) are sometimes visible but only faintly so. Dorsal fin with a pink flush on the spinous part (lappets black), the soft part hyaline with red spots and streaks between the rays, and a narrow basal band of orange-yellow. Caudal fin grey-green, sometimes with pinkish-red streaks between the rays. Anal faintly grey, becoming sooty in the region of the spines and with a very faint pink flush over the soft part, becoming more intense at the distal margin of the anterior part of the fin; ocelli orange red. Pelvic fins dusky.

Sexually active males. Dorsal body surface intense ultramarine to purple with a faint sooty overlay especially along the base of the dorsal fin and over the nuchal region; ventral part of body, from just before the vent to the posterior tip of the caudal peduncle, dark greenish-indigo. Belly, chest and flanks below the level of the lower lateral line crimson, the belly scales with or without a narrow black margin; lower jaw and ventral surface of the head light blue to greenish-blue. Faint traces of transverse bars are sometimes visible on the mid-flank region of the body. The intensity and extent of the red flank and belly colours vary with the emotional state and may be restricted to a small triangular area on the chest extending thence dorsally to a level at about the midpoint of the operculum. The dorsal head surface is always ruddy although the intensity and the area involved are variable; however, the snout and cheeks are invariably reddish. A lachrymal stripe of variable intensity and width is always visible. Dorsal fin is pink to crimson, the colour most intense between the rays; lappets sooty. Caudal fin pink to dusky pink, the colour most concentrated proximally; posterior angles sometimes scarlet with a faint sooty overlay. Anal pink, the margins of the spinous part with a sooty overlay; ocelli orange yellow. Pelvic fins dusky with, usually, a faint pink flush.

Female coloration is also variable. Basically, the body is olive-yellow, darkest dorsally (even becoming grey-blue) and on the cheeks, lightest ventrally on the belly and jaws (almost peach-colour), the flanks sometimes with a pinkish glow. Faint traces of vertical bars are often visible on the flanks and caudal peduncle, the bars usually dark olive green and extending to the dorsal outline of the body.

In excited fishes the colours darken so that the back, dorsal head surface and the vertical flank marks appear very dark olive whilst the flanks and belly become an olivaceous yellow-green; in this condition a dark lachrymal stripe develops. Dorsal fin pale olive yellow with a faint pink flush most concentrated between the spinous and anterior branched rays. In excited individuals the pink colour darkens to scarlet and appears as blotches between the anterior soft rays. Caudal olive-yellow, darker (olive-green to sooty) proximally. Anal buff, sometimes with a faint sooty overlay in the region of the spines; spots (in the position of the ocelli in males) orange. Pelvic fins buff, the anterior half sometimes orange.

Coloration in preserved specimens. Adult males (*sexually active*) light brown, the chest, branchiostegal membrane, lower half to three-quarters of the caudal peduncle and the entire belly sooty, the latter with a silvery overlay. A broad, nearly vertical lachrymal stripe runs from the angle of the jaws to the orbit; the snout is crossed by two transverse bars and there is a medially interrupted nuchal band running upwards from the posterior margin of the orbit. The flanks are crossed by six or seven dark bars, each broadest at its midpoint and narrowing more markedly dorsally than ventrally where it merges with the dark ventral body coloration. All fins (except the pelvics) are hyaline; the lappets of the spinous dorsal are dark, as is the base of the caudal; along the base of the anal fin there is a faint, sooty crescent and near its posterior tip two or three large, circular, greyish ocelli. The pelvics are black.

Sexually quiescent adult males have a similar coloration except that the pearly-silver overlay on the belly is brighter and the lower part of the caudal peduncle is brownish rather than black. The lachrymal, nuchal and cheek stripes are as in active fishes as are the vertical flank bars except that some of the latter extend to the base of the dorsal fin; none extends to the ventral body outline. The fins are as described above but the base of the anal and caudal may be hyaline and the posterior margin of the pelvics light sooty.

Females are grey-brown above, shading to silvery white on the belly and ventral flanks. The lachrymal bar is short (not extending to the jaw angle), the nuchal stripe and snout bars very indistinct or absent. There are five or six faint vertical bars on the flanks, each bar reaching the base of the dorsal fin but not the ventral body outline. All fins are hyaline, the lappets of the spinous dorsal dark.

Ecology. Habitat. Haplochromis annectidens is an inshore species occurring mainly in the vicinity of or amongst the marginal vegetation, and only rarely over exposed sandy beaches away from rooted plants; apparently it does not penetrate deeply into the marginal swamps and is rarely recorded at the swamp ends of inlets.

Food. Data on the food of *H. annectidens* were obtained principally from fourteen preserved specimens which I examined; these observations were supplemented by notes made on four specimens by the C.N.B.S. Despite the small size of these samples the variety of organic material found in the stomach and intestines is high, suggesting that the feeding habits of the species are also varied. Perhaps the commonest gut content is a barely recognisable mush of plant debris, both algal and phanerogamic, with blue-green algae predominating. Such material often forms the flocculent "mud" which covers the bottom in inshore regions of the lake; this leads one to conclude that many fishes had fed from the bottom. This supposition gains support from the presence of dipteran larvae in the stomach contents of the same individuals. Less frequently, the guts contain fragments of plant epidermis (and sometimes the bladders of *Utricularia*) together with large quantities of epiphytic algae, especially diatoms and filamentous green algae (e.g. *Oedogonium*).

These remains suggest that the fishes had been grazing epiphytic algae off submerged plants. Sand grains and fragmentary insect remains also occur in gut contents of this type; it is impossible to tell whether the sand grains were derived from the bottom or whether they were derived from the broken-down cases of Trichoptera larvae. Likewise it is difficult to suggest the provenance of the insect larvae.

As far as could be told from the preserved guts there is little digestion of the phanerogamic material, the blue-green algae or the filamentous green algae; diatom frustules, by contrast, were always empty.

In one specimen the stomach was packed with sand grains but it also contained two larval fishes. Since the larvae were small and not Cichlidae they should, presumably, be listed amongst the food organisms of this species.

Haplochromis annectidens has the long gut ($2\frac{1}{2}$–$2\frac{3}{4}$ times the standard length) and the dentition of a herbivore. It was somewhat surprising, therefore, to find such ill-defined feeding habits. However, it may be recalled that the similar species *H. lividus* and *H. obliquidens* of Lake Victoria are also somewhat facultative in their feeding habits, although in these species there is a predominance of algal grazing over other feeding methods (Greenwood, 1956).

Breeding. One female with embryos in the mouth is recorded by the C.N.B.S. (June 1962); this specimen was not amongst those brought back to the Museum. The sex of the smallest specimen available (43 mm. S.L.) could not be determined, but a male 44·5 mm. S.L. is sexually active although another of 46 mm. is juvenile; the smallest female (50 mm. S.L.) is of undeterminable state but is probably maturing. The largest fishes examined (both 67 mm. S.L.) are of opposite sexes.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. The slender, obliquely cuspidate teeth of *H. annectidens* place it in the well-defined group of East African *Haplochromis* comprising the following species: *H. obliquidens* and *H. lividus* (Lake Victoria) and *H. astatodon* (Lake Kivu). Apart from their peculiar teeth and their long guts, these species have a generalized anatomy. Each differs from the others in a number of characters, including dental morphology. From *H. obliquidens*, with its invariably unicuspid anterior and anterolateral teeth, *H. annectidens* is distinguished by having bicuspid teeth in these positions, and in having teeth which are stouter and with somewhat differently shaped crowns (see fig. 7*d*); the interorbital is narrower in *H. annectidens* (21·0–29·2, M = 25·2%, *cf.* 27·8–34·7, M = 31·8 in *H. obliquidens*) and the cheek shallower (12·5–21·7, M = 18·1% of head, *cf.* 19·0–25·0, M = 21·5). Although the range for the lateral line scale count is identical in both species, the modal number for *H. annectidens* (32) is higher than in *H. obliquidens* (31).

The teeth in *H. lividus* are bicuspid, but crown form serves to distinguish them from those of *H. annectidens*; indeed, the condition in the latter species is almost perfectly intermediate between *H. lividus* and *H. obliquidens* (see fig. 7*c*). *Haplochromis annectidens* and *H. lividus* also differ in certain morphometric characters; the interorbital of *H. lividus* is broader (26·2–33·3, M = 29·7% of head, *cf.* 21·0–29·2, M = 25·2), the cheek is slightly deeper (17·0–24·1, M = 20·1% of head) and the range of lateral line scale counts extends to 34, although the modal number is identical in both species (32). The most pronounced difference lies in the coloration of adult males. *Haplochromis lividus* is probably unique within the genus (and certainly is unique amongst the *Haplochromis* of Lakes Victoria and Nabugabo) for the intense, almost fluorescent blue colour of the head and snout of adult males. This coloration contrasts strongly with the ruddy head tones of *H. annectidens*. (Male coloration also seems to distinguish *H. obliquidens* and *H. annectidens*; *cf.* p. 332 above with p. 229 of Greenwood, 1956).

The dental morphology of *H. annectidens* is very similar to that of *H. astatodon* from Lake Kivu, but there are fewer inner tooth rows in *H. annectidens*. The species also differ in head shape, the gently sloping head profile of *H. annectidens* contrasting with the declivous snout and rounded upper profile of *H. astatodon*; also, in *H. annectidens* the interorbital is markedly smaller than the eye, but in *H. astatodon* of a comparable size the two measurements are equal or the interorbital width is slightly greater.

Trewavas (1933) mentions *H. plagiodon* (a Lake Victoria species) when discussing the affinities of *H. annectidens*, but notes that the teeth of the former are "much larger and fewer", a description with which I concur (see Greenwood, 1959*b*). However, in the introduction to her paper, Trewavas suggests that *H. annectidens* "represents the stock from which *H. obliquidens* and *H. plagiodon* of Lake Victoria seem to have diverged in separate directions". Certainly, *H. annectidens* represents a dental and anatomical grade which could be ancestral to that of *H. obliquidens* but the level of its dental specialization is higher than that likely to be ancestral to the peculiar teeth found in *H. plagiodon* (see Greenwood, 1959*b*). Rather, I would support Trewavas' idea (1933, p. 324) that *H. plagiodon* evolved from a stock resembling *H. velifer* in its dental morphology. The anatomical status of *H. velifer* is that of a generalized *Haplochromis* but it does differ from many of the other generalized species in having somewhat obliquely cuspidate teeth. The *H. plagiodon*-type of tooth represents but a slight modification of the *H. velifer*-type, the *H. lividus-annectidens-obliquidens* types are much more extreme developments involving both the neck and the crown of the tooth.

STUDY MATERIAL

B.M. (N.H.) reg. no.	*Collector*
1933.2.23.210 (Holotype)	Worthington
1933.2.23.211–220 (Paratypes)	Worthington
1935.8.23.111–113	Pitman
1964.7.1.41–79	C.N.B.S.

Haplochromis beadlei Trewavas, 1933

(Text fig. 8)

H. beadlei Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 324.

HOLOTYPE: An adult male 106·0 mm. S.L., from Lake Nabugabo (E. B. Worthington collection), B.M. (N.H.) reg. no. 1933.2.23.221.

Although *H. beadlei* is easily distinguishable from other species of *Haplochromis* in Lake Nabugabo, its systematic status is uncertain. It closely resembles *H. labiatus* of Lake Edward and *H. crassilabris* of Lake Victoria; neither of these species is sufficiently well-known to allow for a full assessment of the characters by which *H. beadlei* differs from them. As is usual amongst related *Haplochromis* species there is no single trenchant diagnostic character; since various combinations of characters (differing for large and for small specimens) seem to distinguish *H. beadlei*, it is retained as a distinct species pending a full revision of *H. crassilabris* and *H. labiatus*, especially the latter.

DESCRIPTION based on the holotype, nine paratypes and thirteen additional specimens, 72–118 mm. standard length.

Depth of body 36·0–40·3 (M = 38·1) per cent of standard length, length of head 31·4–35·8 (M = 33·8) per cent. Dorsal head profile straight or faintly concave, sloping at about 35°–40° with the horizontal; snout straight, not decurved.

Preorbital depth 14·8–18·0 (M = 15·9) per cent of head length, least interorbital width 23·2–28·0 (M = 25·0), snout length 29·6–36·0 (M = 31·7) per cent, snout slightly broader than long or, rarely, as long as broad. Eye diameter 25·0–32·0 (M = 27·8) per cent of head, depth of cheek 17·8–25·6 (M = 22·1) per cent.

Caudal peduncle 13·4–17·0 (M = 15·2) per cent of standard length, 1·1–1·6 (modal range 1·2–1·4) times as long as deep.

Mouth horizontal, both lips markedly thickened, usually to a comparable degree or with the upper lip slightly thicker; in one specimen there is an incipient median lobe developed on the upper lip. Jaws equal anteriorly in most specimens but in a few fishes > 85 mm. S.L. the lower jaw projects slightly so that the upper teeth

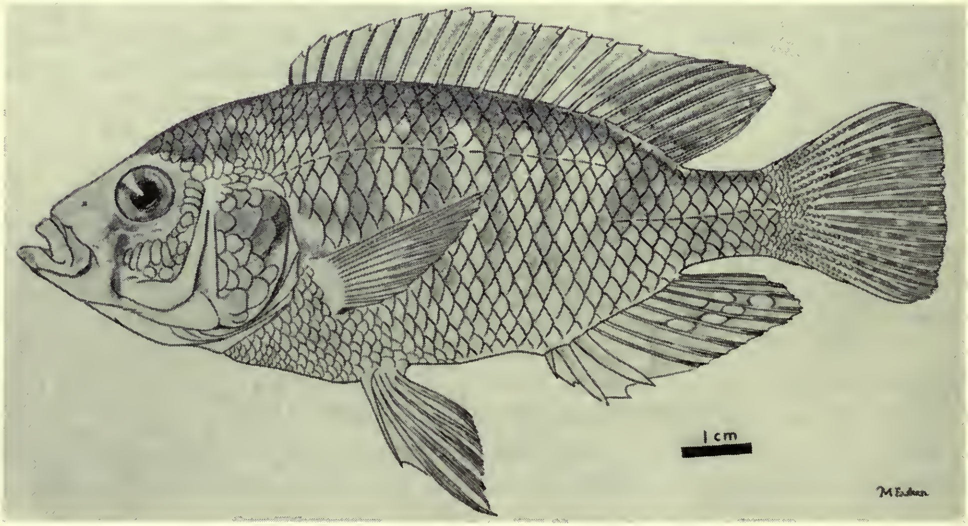

FIG. 8. *Haplochromis beadlei*. Drawn by Miss M. Fasken.

occlude behind the lower. Lower jaw 34·5–39·6 (M = 36·9) per cent of head, 1·3–1·7 (mode 1·4) times as long as broad. Posterior tip of the maxilla somewhat bullate, reaching the vertical through the anterior orbital margin in most specimens but not quite reaching this point in others (33% of the sample examined), rarely extending to below the anterior part of the eye.

Gillrakers variable (except for the lowermost one to three), from moderately slender to moderately stout, but of constant form in any one individual; 7 (f.3), 8 (f.16) or 9 (f.4) on the lower part of the first gill arch, the lowermost one to three rakers reduced.

Scales ctenoid; lateral line with 30 (f.3), 31 (f.14) or 32 (f.5) scales; cheek with 2 (f.4), 3 (f.18) or 4 (f.1) rows; 5–7 (modes 6 or 7) scales between the dorsal fin origin and the upper lateral line, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.11), 25 (f.11) or 26 (f.1) rays, comprising 15 (f.15) or 16 (f.8) spinous and 8 (f.1), 9 (f.16) or 10 (f.6) branched rays; anal with 10 (f.1), 11 (f.4) or 12 (f.18) rays comprising 3 spines and 7 (f.1), 8 (f.4) or 9 (f.18) branched rays. Caudal subtruncate, scaled on its basal half. First two rays of the pelvic fin barely produced in females but greatly elongate in males. Pectoral 23·3–28·0 (M = 26·0) per cent of standard length.

Teeth. The nature of the dentition changes with the size of the individual but is always characterized by the teeth being stout and slightly curved, with the anterior teeth somewhat procumbent (those of the upper jaw most obviously so). The outer, upper teeth are all bicuspid in most fishes <85 mm. S.L. (and in all individuals <75 mm.), those situated anteriorly have subcylindrical crowns but those laterally and posteriorly are more flattened. The anterior and anterolateral teeth in most specimens >85 mm. S.L. are cylindrical in section and are unicuspid or with a poorly developed minor cusp; the crown, especially in unicuspids, is slightly recurved. In exceptional individuals over 85 mm. S.L. (the holotype is one of these) the entire upper outer row is composed of distinctly bicuspid teeth.

The outer row of the lower jaw is, in general, like that of the upper except that the anterior teeth are less procumbent and are often implanted vertically; variations in tooth form follow the same size-correlated trends described above.

There are 24–32 (M = 28) teeth in the outer row of the upper jaw.

Teeth of the inner series are tricuspid and small, and are arranged in 2 or 3 (mode) rows in each jaw. In one exceptional specimen, some of the teeth in the outermost inner row of the lower jaw are enlarged and weakly tricuspid.

The shape of the dental arcade in all specimens is a broadly rounded U.

Lower pharyngeal bone moderately slender, the triangular dentigerous surface slightly broader than long. The lower pharyngeal teeth are compressed, cuspidate and slender, and are arranged in 22–26 rows. In fishes over 80 mm. S.L. the two median rows are composed of coarser and weakly cuspidate teeth. Some of the posterior teeth in neighbouring rows are also enlarged and form a small, roughly triangular zone of enlarged teeth at the posterior end of the median tooth rows; the degree of enlargement undergone by these teeth is positively correlated with the size of the individual.

Vertebrae 28 or 29, comprising 13 abdominal and 15 (f.5) or 16 (f.6) caudal elements.

Coloration in life. Sexually active male. The dorsal surface of the body is greeny-blue (rather more green than blue), the head darkest; flanks lighter, the ventral surface of the chest sooty but the lateral aspects with a red flush. Dorsal fin sooty along its base and over the whole spinous part, the soft part being pink. Anal pink, with a sooty overlay which becomes intensely black over the spinous part; ocelli orange-yellow. Pelvic fins uniformly sooty.

Females are bright olive-green, the flank scales with turquoise margins; belly blueish-green, chest golden olive to silvery white. Dorsal surface of the head dark umber, cheek with golden lights. Dorsal fin pale olive, with a sooty overlay. Anal clear olive-yellow, spots (when present occupying the place of ocelli in males) bright yellow. Caudal fin light olive with dark red maculae between the rays. Pelvics olive with a sooty overlay, the first two rays dead white.

N.B. These colour notes are based on many fewer fishes than are those for the other species; only one sexually active male is described in the C.N.B.S. field-notes.

Coloration of preserved specimens. Adult males (sexually active) are dark brown, almost black, with a pearly sheen on the belly. Lower jaw and branchiostegal membrane are greyish, the cheeks brownish and the operculum dark with a pearly overlay. The snout and dorsal aspect of the head is blackish; there is a distinct lachrymal stripe but no trace of a nuchal band; an ill-defined, blotchy stripe runs along the opercular-preopercular junction. The flanks are crossed by six vertical bars which merge dorsally and ventrally with the dark ground colour of the body. The base of the caudal fin is black, the remainder of the fin becoming progressively lighter towards its posterior margin. The entire spinous dorsal and the basal quarter of the soft dorsal are black to sooty, the remainder of the soft part darkly maculate. Anal fin hyaline, with five large, grey ocelli each outlined by a dark ring. Pelvics with anterior third black, remainder whiteish, the demarcation not well defined.

Sexually quiescent males are brownish, shading to dusky silver on the belly. Lower jaw and branchiostegal membrane are silvery white. A broad, dark lachrymal stripe originates slightly ventral to the jaw angle and continues to the anterior orbital margin; this stripe extends through the eye to form a transverse nuchal band. A weaker, posterior nuchal band is also present and originates at the junction of the operculum and body. The flanks are crossed by six, moderately broad vertical bars which extend to the base of the dorsal fin but do not reach the ventral body outline. The greater part of the dorsal fin is dusky, the soft part weakly maculate. The base of the caudal fin is dark, the rest hyaline. The anal is hyaline with three oval, dead-white ocelli. The pelvics are black on the anterior third, whiteish posteriorly, the demarcation being clear cut.

Females are light brown, becoming silvery white on the belly and ventral aspects of the flanks. The lachrymal stripe is very faint as are the nine, ventrally incomplete vertical bars on the flanks and caudal peduncle; dorsally these bars merge with the base of the dorsal fin, the latter being hyaline with a slight darkening between the posterior spines and between all the soft rays. The distal part of the soft dorsal is often darkly maculate. Caudal fin hyaline with dark maculae; anal hyaline, with three to six small, dead-white ocelli often arranged in two rows. Pelvic fins also hyaline.

Ecology. Habitat. This species is apparently confined to shallow, inshore regions of the main lake and the lakeward ends of inlets to the marginal swamps. The substrate in these places varies, and includes sand, sand with a mud-detritus overlay and deep mud.

Food. The gut contents of eight specimens containing ingested material were examined. All except one contained fragments of insect larvae (chironomid and trichopteran); in one of these fishes the gut yielded numbers of undamaged cases of Trichoptera larvae but in all the others containing identifiable trichopteran remains, no trace of the cases was found. Fragments of undigested plant epidermis were recorded in two specimens. The exceptional fish noted before contained a large amount of unidentifiable sludge.

Breeding. No data are available on the breeding habits of *H. beadlei*. One specimen (a male paratype, 77 mm. S.L.) has cichlid embryos and larvae in its mouth. Because these are at such disparate stages of development it seems unlikely that they represent a brood; rather, I suspect that the adult had snatched at young jettisoned by parents as they were captured, a not uncommon phenomenon (personal observations on the behaviour of netted *Haplochromis* in Lake Victoria).

With one exception, all the specimens examined are obviously adult; the exceptional fish, a female 72 mm. S.L., may be a juvenile or it could be a spent and quiescent adult. There is no sexual dimorphism in the size attained by fishes in this sample.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. The peculiar oral dentition, heavy lips and general morphology of *H. beadlei* indicate a strong affinity with *H. paucidens* (Lake Kivu), *H. crassilabris* (Lake Victoria) and *H. labiatus* (Lake Edward). Unfortunately none of these species is well-known morphologically or ecologically despite, in the case of *H. crassilabris*, intense field studies on the Lake Victoria *Haplochromis*.

The description of *H. labiatus* is based on three specimens of rather disparate sizes (60, 74 and 107 mm. S.L.); no information is available on live colours or ecology. The present concept of *H. crassilabris* stems from twelve specimens and does not agree entirely with that published by Regan (1922); my revision of *H. crassilabris* is still unpublished but will be used here as the basis for comparison with *H. beadlei*. Comparative data for *H. paucidens* were obtained from four specimens in the British Museum (N.H.).

Haplochromis beadlei differs from *H. crassilabris* in the following characters:

(i) In fishes of a comparable size, *H. beadlei* has a relatively smaller proportion of unicuspid to bicuspid outer teeth, and the teeth are more compressed and less cylindrical in cross-section (especially through the neck); also, in *H. crassilabris* some unicuspids appear anteriorly in smaller specimens.

(ii) There are more teeth in the outer row of the upper jaw (24–32, M = 28 *cf.* 20–30, M = 24 for *H. crassilabris*).

(iii) The height of the teeth in the upper jaw of *H. beadlei* is gently graded postero-anteriorly but in *H. crassilabris* the anterior teeth are markedly larger than the lateral ones.

(iv) The lower jaw in *H. beadlei* is somewhat longer (34·5–39·6, M = 36·9% of head, *cf.* 31·0–34·0, M = 32·4 in *H. crassilabris*).

(v) In *H. beadlei* the female has well-defined spots on the anal fin, corresponding in position with the ocelli of males; no spots are developed in *H. crassilabris.*

The orodental characters of *H. beadlei* appear less specialized than those of *H. crassilabris.* However, it is difficult to determine whether the "*beadlei*" condition represents an evolutionary stage intermediate between the generalized *Haplochromis* condition and the "*crassilabris*" level, or whether it is a slightly regressive development from a species which had already achieved the "*crassilabris*" stage. The possibility of such regressive changes must be given serious consideration because this phenomenon has been demonstrated in the cichlid *Astatoreochromis* (Greenwood, 1965). An aquarium bred specimen of *A. alluaudi,* derived from a typical Lake Victoria population, failed to develop the hypertrophied pharyngeal structures characteristic of its ancestors. The degree of hypertrophy shown by the aquarium fish resembled an intermediate stage in the development of this particular specialization. Thus, it seems possible that *H. beadlei* could have evolved from a "*crassilabris*"-like ancestor if environmental conditions in Lake Nabugabo were such that selection pressure did not demand the full expression of the specialized "*crassilabris*" dentition.

From *H. labiatus, H. beadlei* is distinguished by the following:

(i) The large specimen of *H. labiatus* (107 mm. S.L.) has its lower jaw shorter than the upper; in *H. beadlei* of a comparable size the jaws are equal anteriorly or the lower projects slightly.

(ii) At all sizes the eye is about equal to the interorbital width in *H. beadlei* but in *H. labiatus* the eye is distinctly larger.

(iii) In small specimens of *H. labiatus* (60 and 74 mm. S.L.) the teeth are more compressed than those in comparable sized *H. beadlei*; in larger specimens the teeth are identical.

(iv) The upper dental arcade in the large *H. labiatus* is more acutely rounded than in *H. beadlei* but the arcade in small specimens is identical.

(v) The dorsal head profile of small *H. labiatus* is more rounded than in *H. beadlei,* and the snout is more declivous (*ca* 60° *cf.* 35°–40° for *H. beadlei*); in larger fishes these differences are less marked but the profile still slopes more steeply in *H. labiatus.*

Haplochromis paucidens of Lake Kivu is very similar to *H. crassilabris* in gross morphology and dental characters. Thus, it may be distinguished from *H. beadlei* by the same characters (see above); from the few specimens available, the teeth appear to be finer than those of *H. crassilabris* and therefore stand in even greater contrast with those of *H. beadlei.*

The lower pharyngeal bone and its dentition is identical in all three species.

Live coloration is unknown for *H. labiatus* and the only record for *H. crassilabris* is from a 35 mm. colour-transparency (kindly lent to me by N. Mitton of Nairobi).

As far as I can determine, there is a general similarity between the coloration of *H. crassilabris* and *H. beadlei*.

Two other species from Lake Victoria, *H. chromogynos* and *H. chilotes*, should be considered since both species have thickened lips and a dentition obviously related to that of *H. beadlei*. Of the two, *H. chromogynos* has the greater similarity to *H. beadlei*. It is distinguished from the latter species by its fewer teeth, shorter lower jaw (30·0–34·4, M = 32·5% of head) and the fact that all females have a piebald black and silver coloration (Greenwood, 1959*b*). *Haplochromis chilotes* represents a more extreme development of *H. chromogynos*, particularly with regard to the hypertrophy of the lips; most specimens have both lips drawn out medially to form large lobes, although in others there is only an incipient lobation and in a few the lips are little more developed than in *H. beadlei*. (It will be recalled that one specimen of *H. beadlei* has an incipient lobe developed from the upper lip.) Several morphometric characters of *H. chilotes* are correlated with the degree of lip hypertrophy, but even specimens with poorly-developed lips may be distinguished from *H. beadlei* by having a more acute dental arcade, finer teeth and a shorter lower jaw (30·0–36·6, M = 33·2 *cf.* 34·5–39·6, M = 36·9% of head, in *H. beadlei*). On the other hand, the lower jaw of *H. chilotes* with lobed lips is slightly longer than in *H. beadlei* (36·0–49·0, M = 39·6% head). Finally, there are distinctive differences in the live colours of adult males (*cf.* p. 338 above with p. 209, Greenwood, 1959*b*).

As Trewavas (1933) noted, the morphological affinities between *H. beadlei*, *H. crassilabris*, *H. paucidens* and *H. labiatus* are strong; to this complex may now be added *H. chromogynos* which, in turn, bridges the morphological gap between this complex and the more extreme *H. chilotes*. This species complex will be discussed again; for the moment it is only necessary to point out that *H. beadlei* does seem most closely related to *H. labiatus* of Lake Edward and not, as might be expected, to *H. crassilabris* of Lake Victoria. As a corollary to this paradox, the known specimens of *H. paucidens* (Kivu) seem closer to *H. crassilabris* than to the geographically near *H. labiatus* of Lake Edward.

Trewavas (*op. cit.*) also suggested that *H. beadlei* is closely related to *H. sauvagei* of Lake Victoria, a species which, on Regan's revision of the Victoria species, is related to *H. crassilabris*. However, recent studies (Greenwood, 1957) show that *H. sauvagei* belongs to a different lineage and one not closely related to *H. crassilabris*. The jaw structure, skull architecture and dental characters of the *H. sauvagei* line are distinctive and are not even foreshadowed in the *H. crassilabris*-*H. beadlei* species group.

STUDY MATERIAL.

B.M. (N.H.) reg. no.	*Collector*
1933.2.23.221 (Holotype)	Worthington
1933.2.23.222–230 (Paratypes)	Worthington
1933.2.23.231–3	Worthington
1935.8.23.114–134	Pitman
1964.7.1.1–11	C.N.B.S.

Haplochromis venator sp. nov.

(Text fig. 9)

H. pellegrini: (non Regan) Trewavas, 1933, *J. Linn. Soc. Lond.* (*Zool.*), **38** : 326.

Trewavas (1933) identified seven specimens of a predatory *Haplochromis* from Lake Nabugabo as *H. pellegrini* Regan on the basis of a comparison with the two syntypes of *H. pellegrini*. Since 1933 many more specimens of *H. pellegrini* have been obtained and a revised description of the species has been prepared (Greenwood, 1962). It is now clear that the Nabugabo fishes, although showing some affinity with *H. pellegrini*, should be recognised as a distinct species for which the name *venator* is proposed (Venator, Latin, a hunter).

HOLOTYPE: an adult female 158 mm. standard length (B.M. (N.H.) reg. no. 1933.2.23.240) collected by Dr. E. B. Worthington.

DESCRIPTION based on the holotype and twelve paratypes, 59–178 mm. S.L.

Depth of body 28·8–35·5 (M = 32·9) per cent of standard length, length of head 34·6–36·8 (M = 35·5) per cent; dorsal head profile straight or slightly concave (the depression increasing with size and accentuated by the prominent premaxillary pedicels), sloping at 30°–35° to the horizontal.

Preorbital depth 16·3–21·0 (M = 18·9) per cent of head length, least interorbital width 16·8–21·8 (M = 19·0), snout longer than broad, its length 33·6–38·5 (M = 35·3) per cent, probably showing slight positive allometry with standard length. Eye diameter 21·9–28·6 (M = 24·1) per cent of head, showing very slight negative allometry; cheek 19·0 (in the smallest specimen) –28·2(M = 25·6) per cent and showing very slight positive allometry.

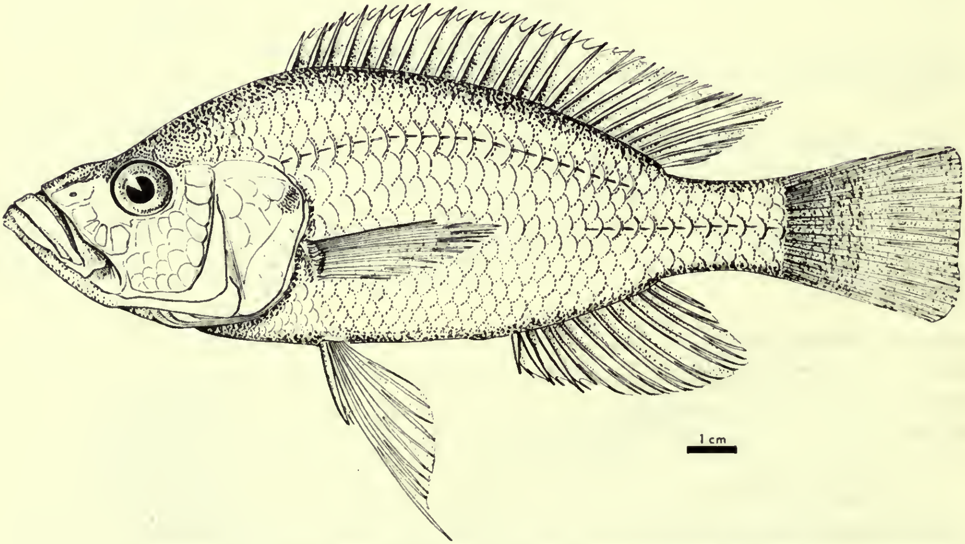

FIG. 9. *Haplochromis venator.* Drawn by Barbara Williams.

Caudal peduncle 14·3–17·5 (M = 15·8) per cent of standard length, 1·2–1·6 (modal range 1·3–1·4) times as long as deep.

Mouth oblique, sloping upwards at about 30°–35°, lips not thickened but the dentigerous surface of the premaxilla expanded antero-posteriorly in the midline. Jaws either equal anteriorly or the lower projecting slightly (both conditions equally common), its length 47·6–54·0 (M = 50·6) per cent of head length, 2·1–2·5 (mode 2·3) times as long as broad. Posterior tip of the maxilla usually not reaching the vertical through the anterior orbital margin (but nearer this point than to a vertical through the nostril), sometimes reaching that point.

Gillrakers moderately stout, the upper three or four usually flattened and anvil-shaped, the lower one to three reduced; 8–10 (mode 9) on the lower limb of the first gill arch.

Scales ctenoid; lateral line with 31 (f.1), 32 (f.9) or 33 (f.3) scales; cheek with 3 or 4 rows; 5–6 (rarely 6½) scales between the dorsal fin origin and the upper lateral line, 5–6 (mode 5) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.5), 25 (f.7) or 26 (f.1) rays, comprising 14 (f.3), 15 (f.8) or 16 (f.2) spinous and 9 (f.3) or 10 (f.10) branched rays. Anal with 12 (f.9) or 13 (f.4) rays, comprising 3 spines and 9 (f.9) or 10 (f.4) branched rays. Pectoral 23·7–27·5 (M = 26·0) per cent of standard length. Caudal subtruncate, the posteroventral corner often obliquely truncate. Pelvics with the first ray produced in both sexes.

Teeth. Throughout the size-range examined, the outer row of teeth in both jaws is composed of slender unicuspids, those situated anteriorly and laterally being slightly recurved, whilst those posterolaterally are more strongly curved and are directed medially. There are 46–64 (M = 53) teeth in the outer row of the upper jaw in fishes 59–128 mm. S.L. (N = 6) and 52–80 (M = 63) in larger individuals (N = 7).

The inner rows are composed of small, unicuspid teeth in fishes > 110 mm. S.L., and of small tricuspid, weakly tricuspid and, predominantly, unicuspid teeth in individuals 59–107 mm. S.L.; the inner teeth are implanted obliquely so that their crowns may come to lie almost horizontally. Inner teeth are arranged in 2 or 3 rows in the upper jaw and 1 or 2 rows in the lower.

Lower pharyngeal bone triangular, the length of the dentigerous surface equal to its breadth or, rarely, slightly longer. The pharyngeal teeth are slender, compressed and weakly cuspidate (some almost caniniform in the median rows of larger fishes) and are arranged in 20–22 rows.

Neurocranium. The neurocranium of *H. venator* closely resembles that of *H. longirostris* and *H. mento*, being intermediate between the two (see Greenwood, 1962); in other words, it has a skull type characteristic of the group of moderately specialized predatory *Haplochromis* in Lake Victoria.

Vertebrae: 29, comprising 13 (f.4) or 12 (f.1) abdominal and 16 (f.4) or 17 (f.1) caudal elements.

Coloration in life. Adult males are bright blueish-green dorsally, shading to silvery on the lower flanks and on the ventral surfaces; operculum and cheek with a pinkish flush. Dorsal fin smokey-grey with a dull red blotch basally at the junction between the spinous and soft parts. Caudal fin sooty grey, the rays darker. Anal sooty at the base of the soft part, the remainder of the fin neutral; ocelli light vermilion-orange surrounded by a narrow white ring, each ocellus set on a transparent area of membrane. Pelvics sooty, darker along the anterior edge.

Adult females have a similar coloration to that of males but the body is a darker, more olivaceous green and the anal fin is olive with a faint salmon-pink flush over the spinous part; as many as five pale red spots occupy the position of the ocelli in males.

Preserved colours. Adult male (*sexually active*): dusky brown except on the belly and chest, which are silver with the scales outlined in black. Dorsal surface of snout dark as are the anterior and anterolateral aspects of the lips, and the branchiostegal membrane; an ill-defined, dark lachrymal blotch is present, and there are very faint traces of six dark, vertical bars on the flank and caudal peduncle. Dorsal fin grey, with black lappets and a narrow black basal stripe along the origin of the branched rays and the last few spines; the membrane between the soft rays is dark except for a narrow, whiteish band immediately above the dark basal one. Anal fin with a black basal band which is capped by a narrower, dead-white band; the ocelli are very faint. Caudal fin greyish to sooty. Pelvics sooty, darkest along the anterior quarter.

Females: greyish-brown to silvery brown (depending on fixative used, the former for formol, the latter for alcohol), shading to silvery white on chest and belly. Snout, lips and dorsal head surface dark grey or brown. A broad mid-lateral band visible on the flanks in formol fixed specimens only; the band is faint and appears interrupted at about its mid-point.

All fins are hyaline, the anal with faint spots in the position of the ocelli in males; the membrane between the caudal rays is maculate, the spots darkest proximally.

Ecology. Habitat. Haplochromis venator is widely distributed in the lake but appears to be more abundant in open, off-shore areas than in other regions. It has been caught in surface gill-nets set in the middle of the lake over a deep mud bottom (water depth 10 ft.) but is not recorded from bottom nets in the same places, nor from the inlets to swampy areas. Specimens caught in beach operated seines are smaller (30–90 mm. S.L.) than those caught off-shore but this may be a reflection of the type of gear used in the two places.

Food. In addition to data from the C.N.B.S. field-notes, I have examined seven preserved specimens. From these records it is clear that *H. venator* is predominantly a piscivorous predator, although insects (especially adult Ephemeroptera) are also eaten. Only two specimens of the fourteen for which detailed gut analyses are available contained other ingested material, in both cases a few fragments of plant tissue. *Haplochromis* (of *ca* 20–40 mm. total length) and small *Barbus* species seem to be the commonest prey species but in some cases the fish remains were too fragmentary to allow for further identification. One fish (a juvenile 59 mm. S.L.) contained twelve larval cichlids of various sizes but all were within the size range at which larvae are carried by the parent; it is impossible to tell whether such small individuals represent "normal" prey for *H. venator* or whether they were jettisoned young swallowed whilst the seine net was being brought to the shore.

Breeding. No data are available. The two smallest specimens (59 and 82 mm. S.L.) are juveniles; all others are adults (and predominantly females) in differing states of sexual activity.

Distribution. Known only from Lake Nabugabo.

Diagnosis and affinites. The resemblance between *H. venator* and *H. pellegrini* of Lake Victoria has been noted already (p. 342). Several small differences serve to distinguish the two species. In addition, *H. venator* reaches a much larger adult size than does *H. pellegrini* (178 mm. S.L. *cf.* 104 mm.); considering the ecological differences obtaining in the two lakes, this difference is difficult to evaluate. This size difference may underlie a number of the observed morphometric differences between the species. *Haplochromis venator* has a longer lower jaw than *H. pellegrini* (47·6–54·0, M = 50·6% of head, *cf.* 42·3–51·5, M = 46·8 in *H. pellegrini*), a longer pectoral fin (23·7–27·5, M = 26·0% of standard length, *cf.* 19·4–25·3, M = 21·3), and a slightly narrower head as measured by interorbital width (16·8–21·8, M = 19·0% of head, *cf.* 18·2–24·0, M = 21·0 in *H. pellegrini*). In dental morphology the species hardly differ except that unicuspids occur in the inner rows of *H. venator* at all sizes. No inner unicuspids are found in *H. pellegrini*, although in some specimens a few inner teeth may be only weakly tricuspid. The pharyngeal dentition is similar in both species.

A most marked difference is the coloration; live female *H. pellegrini* are a dark chocolate-brown (shading to light brown ventrally) and have greyish-black fins (see Greenwood, 1962). The body of *H. venator* females is olivaceous green shading to silver, the fins are olivaceous to sooty and the anal has a pink flush. Live colours of male *H. pellegrini* are unknown but the dark brown coloration of preserved specimens contrasts with the lighter colours of preserved male *H. venator*.

Neurocranial architecture differs in the two species, the neurocranium of *H. pellegrini* being of a rather distinctive type (see Greenwood, *op. cit.*), whereas that of *H. venator* is closely allied to the *H. mento* and *H. longirostris* types.

The overall morphology of *H. venator* is not closely similar to that of *H. longirostris* from which species it is distinguished by its deeper body, longer and less oblique lower jaw, medially expanded premaxilla and, most obviously, by its shorter and deeper caudal peduncle (14·3–17·5, M = 15·8% of standard length, length/depth ratio 1·2–1·6, modal range 1·3–1·4, *cf.* 17·2–22·2, M = 19·2, 1·9–2·0 modal range, for *H. longirostris*). There are also interspecific differences in dental morphology, especially the finer and more numerous outer teeth of *H. longirostris*.

Haplochromis mento is so obviously distinct from *H. venator* that no detailed comparison is required (see Greenwood, *op. cit.*).

Some resemblance exists between *H. venator* and the group of Lake Victoria *Haplochromis* comprising the "species" *H. macrodon*, *H. taeniatus* and *H. lamprogenys*. This group is under revision, hence the uncertainty as to the specific status of its members. *Haplochromis venator* differs in having more numerous teeth, a somewhat larger eye and narrower interorbital (eye diameter equals interorbital width in the *H. macrodon* group but is larger than the interorbital in *H. venator*) and a longer and more oblique jaw; there are also differences in preserved coloration. Looked at in relation to the morphological groupings of the Lake Victoria predatory *Haplochromis*, *H. venator* belongs to a more specialized grade than does the *H. macrodon* group.

STUDY MATERIAL

B.M. (N.H.) reg. no.	*Collector*
1933.2.23.240 (Holotype)	Worthington
1933.2.23.234–239 (Paratypes)	Worthington
1964.7.1.80–85 (Paratypes)	C.N.B.S.

Haplochromis nubilus (Blgr.) 1906

(Text fig. 10)

Tilapia nubila Blgr., 1906, *Ann. Mag. nat. Hist.*, (7), **17** : 450.

Haplochromis nubilus (part): Regan, 1922, Proc. Zool. Soc., 164 (excluding *Paratilapia victoriana* Pellegrin, 1903, for which see Greenwood, 1962).

Haplochromis annectidens (part) Trewavas, 1933, *J. Linn. Soc. Lond.* (*Zool.*), **38** : 323.

This synonymy is by no means definitive since a revision of the species is still incomplete; it is given here especially to include the two paratypical specimens of *H. annectidens* which are now identified as *H. nubilus*.

From the information I already have on this rather widely distributed east African species there are indications that the various geographical groups may be differentiable on certain anatomical and morphometric characters (see also Trewavas, 1933). Thus, a brief description and tabulation of these characters is given for the five specimens from Lake Nabugabo. The paratypes of *H. annectidens* are indicated with an asterisk.

S.L.	Depth†	Head†	Po.%	Io.%	Snt.%	Eye%	Cheek%	Lj.%	C.P.†
62·5*	39·2	33·6	14·3	28·6	28·0	28·6	23·8	38·1	14·4
65·0*	35·4	32·3	14·6	26·2	31·0	29·2	23·8	38·4	16·8
72·0	37·5	34·7	16·0	24·0	30·0	28·0	20·0	40·0	13·9
86·0	37·2	35·0	16·7	24·4	31·7	26·7	21·7	40·0	15·2
86·0	34·9	35·5	14·7	23·0	31·1	29·6	19·7	39·3	14·0

† = per cent of standard length.
% = per cent of head length.

Caudal peduncle 1·1–1·6 times as long as deep.

Dorsal head profile straight but usually with a marked concavity above the orbit.

Mouth horizontal or very slightly oblique, the lips somewhat thickened; posterior tip of the maxilla reaching the vertical through the anterior margin of the orbit. Jaws equal anteriorly, the lower 1·6–2·0 times as long as broad.

Gillrakers: 8 or 9 (7 in one specimen), relatively stout, on the lower part of the first gill arch, the lowermost 3 or 4 rakers reduced.

Scales ctenoid; lateral line with 31 (f.4) or 32 (f.1) scales, cheek with 3 rows; 6 scales between the dorsal fin origin and the upper lateral line, 5 (f.3) or 6 (f.2) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.2) or 25 (f.3) rays, comprising 15 (f.3) or 16 (f.2) spinous and 9 (f.4) or 10 (f.1) branched rays. Anal with 12 (f.3) or 13 (f.2) rays comprising 3 spines and 9 (f.3) or 10 (f.2) branched rays. Pectoral 23·6–28·8 per cent of standard length. Caudal distinctly subtruncate or rounded. Pelvics with the first branched ray slightly produced in both sexes.

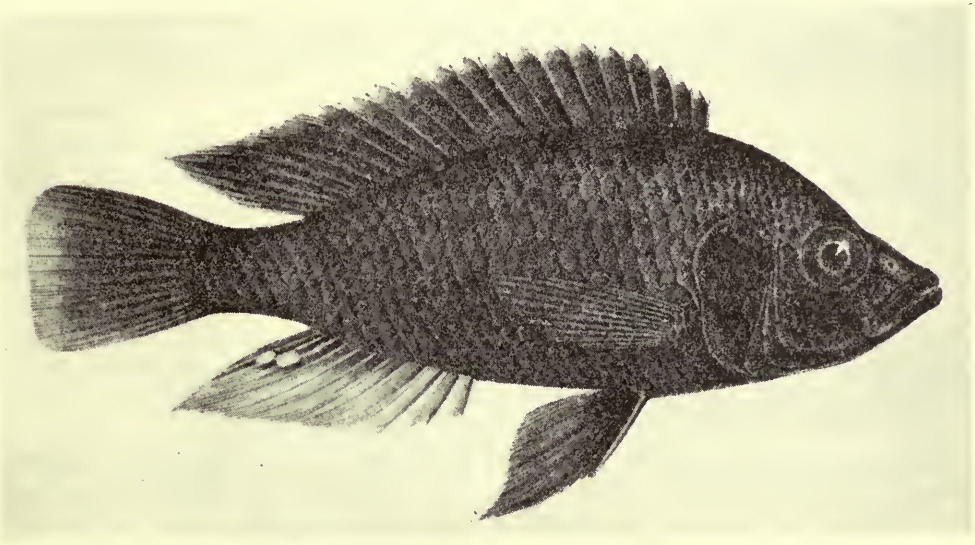

FIG. 10. *Haplochromis nubilus*. From Boulenger, *Fishes of the Nile:* a Lake Victoria specimen is depicted.

Teeth in the outer row of both jaws relatively stout, immovably implanted and unequally bicuspid; the major cusp slopes somewhat obliquely (*cf. H. velifer*). The posterior three or four teeth on either side of the upper jaw are stouter than the anterior teeth and are unicuspid. The number of upper, outer teeth in the five specimens is 40, 42 and 46 (f.3).

The inner rows in both jaws are composed of small tricuspid teeth arranged in 2, 3, 4 or 5 series in the upper jaw and 2 or 3 series in the lower jaw; with one exception, the inner series are separated from the outer row by a distinct interspace; in the exceptional specimen the gap is obscured by the irregular arrangement of the inner series.

Lower pharyngeal bone slender and triangular, its dentigerous surface broader than long. The pharyngeal teeth are slender, bicuspid and laterally compressed, those of the two median rows somewhat coarser. The teeth are fairly close-set (especially in the upper corners of the bone) and are arranged in 24–26 rows.

Coloration. Judging from the few notes prepared by the C.N.B.S. there does not seem to be any noticeable difference in the colours of Nabugabo fishes. Adult males have an overall velvety black colour, with a bright scarlet margin to the entire dorsal fin, scarlet maculae on the soft part, a scarlet distal half of the caudal fin and a similar colour spread over the entire anal fin; the anal ocelli are orange-yellow. The pelvic fins are black.

Ecology. Because so few specimens of *H. nubilus* were recorded by the C.N.B.S. little is known about the habits of this species in Lake Nabugabo. The one locality at which *H. nubilus* was caught is in shallow water (about 3 ft. deep) over a sand and mud bottom and a few feet away from a swamp shore.

No data are available on the food of the Nabugabo population, nor is anything known about their breeding biology except that all five specimens described above are adults (4 males, 1 female).

III. ***HEMIHAPLOCHROMIS*** Wickler, 1963

See Wickler (1963) for a full discussion of this genus.

Hemihaplochromis multicolor (Schoeller) 1903

(Text fig. 11)

Chromis multicolor Schoeller, 1903, *Bl. Aq. Terrk.*, **14** : 185.
Paratilapia multicolor: Hilgendorf, 1903, *Sitzber. Ges. Naturf. Fr. Berlin*, 429–32.
Haplochromis multicolor: Regan, 1922, *Ann. Mag. nat. Hist.* (9), **10** : 249–64.
Hemihaplochromis multicolor: Wickler, 1963, *Senk. biol.*, **44** : 83–96.

As yet, insufficient revisional work has been done on this widespread species to determine the relationships of the Nabugabo population. The C.N.B.S. field notes on coloration certainly do not suggest that the Nabugabo fishes differ in this important character.

Hemihaplochromis multicolor is recorded from the White Nile, Lower Nile, Bahr el Jebel, Lake Albert, the Semliki river, Lakes Victoria and Kyoga, the Malawa and

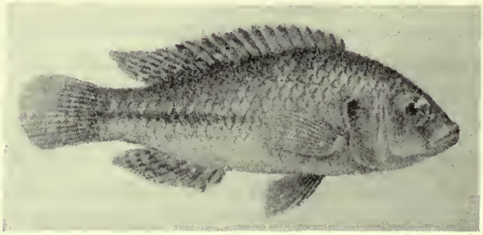

FIG. 11. *Hemihaplochromis multicolor.* From Boulenger, *Fishes of the Nile:* a Lake Victoria specimen is depicted.

Aswa rivers (Uganda) and the small, swampy lakes Kachira, Kijanebalola and Nakavali which lie between Lakes Edward and Victoria. The C.N.B.S.'s material constitutes the first record of the species from Lake Nabugabo.

In Nabugabo, *H. multicolor* was collected from a range of habitats; indeed, it is probably the only *Haplochromis*-group species to occur in the isolated pools of the floating border swamp and in the sand-bar swamp at the eastern lake edge. It is found frequently amongst the rooted vegetation fringing the main lake, and there are records of it from the deep inlets, which penetrate into the swamps. A few specimens were caught amongst flooded tree roots at the mouth of the Juma river. There are no records from the open lake but limitations imposed by the gear used there, coupled with the small size of the fishes, would reduce the chances of their being captured.

The C.N.B.S. concluded that *H. multicolor* are most common in areas where the water is relatively sheltered and where there is a good growth of water-weed, particularly *Utricularia* and *Ceratophyllum*. Of all the species in Lake Nabugabo, *H. multicolor* seems to be peculiar in exploiting *Utricularia* as a food source; presumably it is the animals trapped by the plant, and not the plants, which provide the nourishment.

The feeding habits of *H. multicolor* are diverse. Data from the C.N.B.S. notes indicate that many individuals had fed exclusively on other fishes, especially the cyprinodont *Aplocheilichthys pumilus* and species of the cyprinid *Barbus*. Insects (particularly chironomid and ephemeropteran larvae) and Crustacea (*Cyclops* and Ostracoda) are also recorded, as are some specimens in which the entire gut is packed with filamentous and blue-green algae, or with a mixture of algae and the remains of *Utricularia*. In these latter fishes remains of small Crustacea are also found, suggesting that they were derived from the *Utricularia* bladders since similar animals are trapped by these plants. A few specimens contained, in addition to the plant matter, a number of small oligochaet worms.

No breeding females were recorded by the C.N.B.S., but several females had ovaries in an advanced stage of oogenesis.

IV. *ASTATOREOCHROMIS* Pellegrin, 1903

See Greenwood (1959*a*) for a complete generic synonymy and a discussion of generic characters; also, see Greenwood (1965) for further comments on the generic diagnosis.

Astatoreochromis alluaudi Pellegrin, 1903

(Text fig. 12)

For synonymy see Greenwood (1959*a* and 1964).

A single specimen of this species was collected by the C.N.B.S. and it represents the first record from Lake Nabugabo. Unfortunately it is impossible to be certain that *A. alluaudi* forms a natural element in the Nabugabo fauna. In recent years this species has been introduced into several ichthyo-faunal regions of east Africa as a biological control agent against snails. However, I can find no definite record of introduction to Lake Nabugabo and since it does occur naturally in other small lakes (Greenwood, 1959*a*) and because snail control in Nabugabo would not be necessary (snails are reputedly rare) the evidence does seem to favour the consideration of *A. alluaudi* as a natural element.

The specimen available is an adult male 85 mm. S.L. (85 + 22 mm. total length) and does not differ in any morphometric characters from specimens described before (Greenwood, 1959*a*).

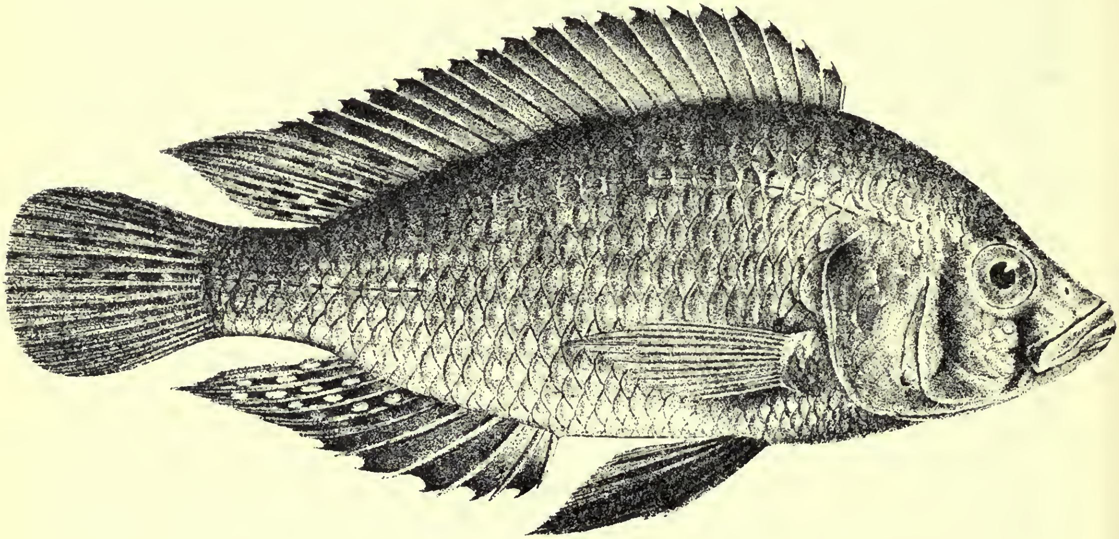

FIG. 12. *Astatoreochromis alluaudi*. From Boulenger. *Fishes of the Nile*.

The oral dentition is likewise typical. The pharyngeal bones and teeth are directly comparable with the greatly reduced type characterizing fishes from Lakes Edward, George, Nakavali and Kachira (*i.e.* of the populations formerly described as the subspecies *A.a.occidentalis*; but see Greenwood, 1965). The lower pharyngeal bone is weak and only slightly enlarged but the upper pharyngeal bones are relatively stouter. The two median rows of lower pharyngeal teeth are composed of slightly enlarged teeth still with remnants of the smaller cusp (*i.e.*, not of the broad-crowned unicuspid type found in specimens from Lake Victoria and in some from Lake Edward). The remaining teeth are small, compressed and weakly bicuspid with the major cusp very prominent. Some enlarged teeth occur on the upper pharyngeal bones and these are relatively stouter than their counterparts on the lower bone; however, they are distinctly bicuspid.

The neurocranial apophysis for the upper pharyngeal bones is markedly reduced in size, with proportionately much smaller basioccipital facets than are found in any other natural population of the species. Indeed, the morphology of the apophysis is comparable with that of an aquarium raised specimen which was fed on a snail-free diet (see Greenwood, 1965).

Unfortunately, the gut of the unique Nabugabo specimen is empty so no data are available on its feeding habits. The extreme scarcity of snails in the lake suggests, however, that the food of these fishes would not be at all like the predominantly snail diet of the Lake Victoria population, and it probably contains even fewer snails than does the diet of populations from Lake Edward.

It is clear from the C.N.B.S. notes that the coloration of the Nabugabo fish is identical with that of specimens from other areas. Like males from Lake Kachira, the Nabugabo fish is adult at a smaller size than has been recorded from Lake Victoria. No data are available on the minimum sizes of adult males from other localities.

DISCUSSION

Before discussing the evolutionary aspects of the Lake Nabugabo *Haplochromis*, it is necessary to consider the status of the five endemic "species", particularly their status *vis à vis* related species in Lake Victoria.

But for one exceptional species pair, the endemic *Haplochromis* are easily distinguished from each other both anatomically and with regard to male breeding coloration. No intermediate specimens are encountered and there is no *prima facie* evidence to suggest that interspecific crossing takes place.

The exceptional pair is *H. simpsoni* and *H. velifer*. There, the overall level of morphological differentiation, although appreciable, is slight and concentrated in dental characteristics. Two specimens out of a total of seventy have a dentition which could be considered a mixed "*velifer-simpsoni*" type; however, each fish has a greater ratio of "*simpsoni*" to "*velifer*" characters. In other respects the morphology of these fishes is "*simpsoni*"-like, but it must be remembered that it is in dental characters that specimens of the two species show the greatest divergence. With only this evidence on which to work, one cannot decide if specimens with apparently interspecific dental characters are of hybrid origin. Whatever their origin, their frequency is very low.

The real problem posed by the Nabugabo species flock is to estimate the degree of biological separation existing between the endemic Nabugabo species and those *Haplochromis* endemic to Lake Victoria which are morphologically closest to them and from which the Nabugabo species were probably derived. Phenotypically, as we have seen, there is every reason to consider them specifically distinct. Indeed, the morphological gaps between any one Nabugabo species and its counterpart in Victoria are as great as those between any two related *Haplochromis* in Lake Victoria. Similar differences are apparent when Nabugabo species are compared with species from Lake Kivu or Lake Edward.

I believe that the marked differences in male coloration between the anatomically nearest species of Nabugabo and Victoria suggest that members of each pair or group would behave as biological species should they ever become sympatric. Ethological studies (Baerends and Baerends van Roon, 1950; Wickler, 1963) all stress the importance of male coloration in species discrimination amongst cichlids; indirect evidence from the multispecific *Haplochromis* flock of Lake Victoria adds support to the experimental studies because one repeatedly finds distinctive male colours characterising otherwise phenotypically similar species.

This evidence is inferential with regard to the extralacustrine validity of the Nabugabo species but it seems as well-grounded as any such evidence can be.

The history of Lake Nabugabo (see page 316) makes it seem unlikely that its fishes were derived from any source other than Lake Victoria, a conclusion amply supported by the non-cichlid fishes.

If this source is accepted, it then remains to consider the stage of speciation which the Victoria *Haplochromis* had reached 4,000 years ago. Allowing for some inevitable genetical differences, it seems likely that there was little major difference between the species then and now. The reasons for my thinking this are based mainly on the difficulty of understanding how any significant number of species could have evolved in Lake Victoria during that short period. If it be argued that some degree of habitudinal isolation would allow for the differentiation of species, then one is faced with the problem of how the species then became widely distributed around the extensive shores of Victoria. Also militating against the concept of habitudinal isolation is the fact that no morphologically distinct populations are recognisable in any present-day Victoria species. This does not, of course, deny the possibility of there being genetically distinguishable populations (particularly since Victoria *Haplochromis* species are usually restricted in their habitat preferences) but the present argument is concerned with the morphological expression of the genotype and the recognition of species in that way.

If habitudinal segregation be ruled out, what of isolation through changes in the topography of the Lake basin? Again there is nothing to support the hypothesis; all the geological and climatological evidence strongly suggests that there has not been any great change in the form of Lake Victoria during the past four thousand years. The problem of intralacustrine distribution after speciation is also relevant.

Thus, it seems reasonable to conclude that at the time of its formation Lake Nabugabo would have been populated by *Haplochromis* similar to those inhabiting a comparable bay in the Lake Victoria of today.

Trewavas (1933) implies that the Nabugabo endemics are relict species. Her views were influenced by the fact that the extreme youth of Nabugabo had not then been fully appreciated, and also by the lack of knowledge about the *Haplochromis* species-flock of Lake Victoria. For instance, it was not realised that there are species in Victoria which, anatomically speaking, are of stock status when compared with the more specialized species existing alongside them, often in the same habitat. This ancestor-descendant relationship is found in all the trophic groups of Victoria *Haplochromis* but is seen especially well amongst the algal grazers, mollusc crushers, mollusc shellers and the piscivorous predators. There is no reason to consider *H. annectidens* anatomically more "basal" than its relative in Lake Victoria, *Haplochromis lividus* (see above, p. 334); *Haplochromis venator* belongs to the Lake Victoria species group containing some of the more advanced piscivorous predators, and there is nothing about *H. simpsoni* or *H. velifer* either more or less specialized than in similar species of Lake Victoria.

The case of *H. beadlei* is equivocal (see p. 340) since although the dental characters of this species seem less specialized than those of *H. crassilabris* in Victoria, they could be interpreted as having evolved, through regression, from a "*crassilabris*"-like condition.

If the endemic *Haplochromis* of Lake Nabugabo were evolved from Lake Victoria *Haplochromis* virtually identical with those of the present day, the evolutionary process was simply one of speciation. It did not involve the development of new adaptive lines from the point of view of feeding mechanisms; indeed, this could hardly have been possible since the Victoria flock had already exploited this field to saturation. Adaptation seems more likely in those physiological characters concerned with respiration and osmoregulation, because the hydrology of Lake Nabugabo certainly differs from that of Victoria.

Historically, Nabugabo is a cut-off bay of Lake Victoria. If, on this basis, it is compared with a bay of comparable size in Victoria, one of the more remarkable features is the reduction in the number of *Haplochromis* and *Haplochromis*-group species: eight species compared with at least thirty in Victoria (i.e. *ca.* 25 per cent of species one might expect to find). There is also a reduction in the number of trophic types amongst the species (four compared with six in Lake Victoria). The broad specializations not represented in Lake Nabugabo are the embryo and larval-fish eaters and the mollusc shellers; there is, also, a reduction in the number of intra-group specializations represented in the Nabugabo flock. Another difference is in the proportions of the various trophic types; the number of insectivorous species in Nabugabo is proportionately much higher than would be found in a bay of Lake Victoria. There, piscivorous species would be most numerous, followed by phytophagous, mollusc-eating and insectivorous species in about equal proportions. These proportions are based on adult and subadult fishes because the feeding habits of immediately post-larval individuals are still unknown.

The non-cichlids of Lake Nabugabo, on the other hand, show much less depauperization, with about seventy-three per cent of the Victoria species also occurring in Nabugabo (figures based on the C.N.B.S. collections now deposited in the B.M. [N.H.].).

There is no indication of the fate of those Lake Victoria trophic groups which are not represented in Lake Nabugabo. Some may have retreated from the embryo lake before it was completely sealed-off and others may have been unable to survive the hydrological changes which took place once the bar was completed, hydrological changes directly affecting the water chemistry or acting indirectly through altered food chains.

The history and ultimate differentiation of the surviving isolated populations provide a text-book case of geographical isolation resulting in speciation. The rate at which speciation occurred shows how rapidly a genetic revolution (*sensu* Mayr, 1963) can be achieved. In relation to the species of Lake Victoria, those of Nabugabo must be considered inferential but it is significant that the degree of morphological differentiation achieved is as great as that existing between related sympatric species in Lake Victoria. The marked differences in male coloration between similar species in the two lakes is striking and, I believe, an important element in providing interspecific barriers. In Lake Nabugabo there could have been no selection in favour of strengthening such potential interspecific barriers because the species evolved there were derived from fully differentiated Victoria species. In such circumstances differences in male coloration must be looked upon as coincidental results of the genetical revolution undergone by the isolates, possibly even byproducts of selection acting on other components of the genotype directly concerned with adaptation to altered and altering environmental conditions.

If these suppositions are accepted, they throw some light on the rate at which genetical isolating mechanisms could evolve in isolated populations of *Haplochromis*. This is one of the principal problems involved in any attempt to explain the evolution of such multispecific flocks as that of Lake Victoria.

Recently, Hubbs (1961) has criticized the emphasis I placed on the role of spatial isolation (i.e. geographical and physical) in accounting for the history of the Lake Victoria *Haplochromis* flock. Lake Nabugabo seems to provide a "pertinent indication" (Hubbs' phrase) of speciation through geographical isolation which Hubbs did not consider when arguing against this concept in favour of essentially sympatric speciation within cichlid flocks. Hubbs believes that "in general, shallow ponds are not scenes of extensive speciation . . . ." and that "No great diversity has arisen within small lakes and ponds over Africa". Perhaps Hubbs was placing much emphasis on the qualifying words "extensive" and "great"; neither, I agree, applies to Nabugabo. However, the fact that speciation seems to have occurred in Nabugabo should be considered and the evidence for it is as good as it is for any allopatric species; it could hardly be more pertinent to the problem of cichlid speciation in Lake Victoria (see Greenwood, 1959*c*). The question of diversity is another issue if the word is taken to cover more extensive evolution than just the multiplication of species. Because of the highly differentiated species-flock from which it arose one would not expect to find great new diversity amongst the Lake Nabugabo species. Nabugabo provides evidence for phylogenesis and not anagenesis. The latter will always be a function of the adaptive levels attained by the ancestral stock or stocks and the environmental conditions obtaining during the evolutionary period under consideration.

The effects of ecological segregation (and with it in many cases spatial but not physically insuperable segregation) on the species of Lake Victoria has certainly been much less marked than has the effect of physical isolation on the ancestors of the present-day Nabugabo species. Lake Nabugabo was cut off about four thousand years ago and in that period the physiography of Lake Victoria has remained unchanged. The Victoria *Haplochromis* species must then have had virtually the same intralacustrine distribution and habitat preferences as at present, yet none has shown any differentiation comparable with that undergone by the populations isolated in the bay that was to become Lake Nabugabo. Any argument that the present-day Victoria species-flock has also evolved and reached the present pattern of species distribution (no species shows a geographically restricted intralacustrine distribution) in the last four thousand years, seems inconceivable in the light of evidence we have on the *Haplochromis* of Lakes Victoria and Edward (particularly the species common to both lakes), and the geological history of the area (Greenwood, 1951, 1959*a* and *c*).

KEY TO THE GENERA OF *CICHLIDAE* IN LAKE NABUGABO

	Scales ctenoid	1
	Scales cycloid	***TILAPIA***
1	Anal fin with three spines	2
	Anal fin with more than three spines	***ASTATOREOCHROMIS***
2	Many scales in lateral line series without pores; no ocelli on anal fin in adult males but posterior tip of fin with pigmented spot	***HEMIHAPLOCHROMIS***
	All scales in the lateral line series with pores; ocelli on anal fin in adult males, no pigment spot on posterior tip	***HAPLOCHROMIS***

KEY TO THE SPECIES OF *HAPLOCHROMIS*

	Lower jaw more than 47 per cent of head length; teeth unicuspid and moderately stout, more than 40 in the upper jaw	***H. venator***
	Lower jaw less than 47 per cent of head length; teeth generally bicuspid or if unicuspid, either slender and numerous or stout and fewer than 40 in upper jaw	1
1	Caudal truncate or weakly subtruncate	2
	Caudal distinctly subtruncate or, more usually, rounded; adult males jet black	***H. nubilus***
2	Teeth bicuspid or unicuspid (or a mixture of both); if predominantly unicuspid, then slender and more than 30 in upper jaw; lips not markedly thickened	3
	Teeth unicuspid or bicuspid, stout and procumbent, less than 34 in upper jaw; lips markedly thickened (upper sometimes thicker than lower)	***H. beadlei***
3	Teeth distinctly bicuspid	4
	Teeth weakly bicuspid or unicuspid or a mixture of both types, slender; more than 50 in upper jaw	***H. simpsoni***
4	Teeth moderately stout, distinctly bicuspid, immovably implanted; major cusp not protracted towards symphysis, and occlusal surface not horizontally aligned	***H. velifer***
	Teeth with slender shafts, weakly bicuspid, major cusp expanded, obliquely truncated so that occlusal surface is almost horizontal and produced towards the symphysis; moveably implanted	***H. annectidens***

SUMMARY

1. Lake Nabugabo, a small swampy lake, is separated from Lake Victoria by a relatively narrow sand-bar and swamp. The sand-bar is estimated to be about 4,000 years old; prior to that date the lake was a bay of Lake Victoria. A short description of the lake and its history is given.

2. The cichlid fishes are reviewed, mainly on the basis of new material collected by the Cambridge Nabugabo Biological Survey of 1962.

3. Six species of *Haplochromis* (five endemic to the lake) are now recorded; of these, two are new (*Haplochromis simpsoni* and *H. venator*; the latter was previously confused with *H. pellegrini* of Lake Victoria) and one (*H. nubilus*) is recorded for the first time.

4. Two other new records are: *Hemihaplochromis multicolor* and *Astatoreochromis alluaudi*. The latter species shows certain interesting osteological differences when compared with specimens from Lakes Victoria and Edward.

5. The evolutionary history of the Nabugabo *Haplochromis* is discussed. The evidence strongly suggests that the endemic species were derived from Lake Victoria species similar to, if not identical with species still extant in Lake Victoria. The significance of this rapid speciation in understanding speciation in Lake Victoria *Haplochromis* is considered.

ACKNOWLEDGEMENTS

In many respects this paper should be regarded as a joint effort between the members of the Cambridge Nabugabo Biological Survey and myself. I have drawn heavily upon their extensive and detailed field-notes as well as on the numerous coloured drawings they made of live fishes. Without their painstaking attention to detail and deep appreciation of the *Haplochromis* problem it would have been almost impossible to gain a full impression of the Nabugabo species. To the members of the C.N.B.S., Alan Roberts, Barney Hopkins, Michael Simpson and Robin Sturdy, I express my warmest thanks.

My thanks are also due to my colleagues, Dr. Ethelwynn Trewavas for the numerous discussions we have had about these fishes, and Mr. A. C. Wheeler for making several radiographs.

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